

# JOURNAL OF THE BOMBAY NATURAL HISTORY SOCIETY

1963 APRIL

Vol. 60

No. 1

## The Asian Weaver Birds: Problems of co-existence and evolution with particular reference to Behaviour

BY

JOHN HURRELL CROOK<sup>1</sup>

*Sub-Department of Animal Behaviour, Zoological Laboratory, Cambridge*

(With two plates, five text-figures, and three  
diagrammatic schemes)

### CONTENTS

	PAGE
I. INTRODUCTION	
a. Aim .. .. .	2
b. Study area—the Kumaon tarai .. .. .	2
c. Field methods .. .. .	4
II. NEW OBSERVATIONS ON TWO WEAVER SPECIES IN INDIA	
a. <i>Ploceus benghalensis</i> .. .. .	4
b. <i>Ploceus manyar</i> .. .. .	10
III. PROBLEMS OF PLOCEINE SYMPATRY IN ASIA, WITH PARTICULAR REFERENCE TO THE TARAI	
a. Habitat selection .. .. .	19
b. Food preferences .. .. .	22
c. Mate selection .. .. .	23
d. Conclusions .. .. .	31
IV. THE EVOLUTION OF THE ASIAN WEAVERS	
a. The African origin of the Asian Weavers .. .. .	32
b. Dispersal and adaptive radiation .. .. .	35
c. The origin and nature of the behavioural differences .. .. .	39
d. Species grouping .. .. .	42
V. SUMMARY .. .. .	43
ACKNOWLEDGEMENTS .. .. .	44
REFERENCES .. .. .	45
APPENDIX .. .. .	47

<sup>1</sup> Present address: Department of Psychology, Bristol University.

## I. INTRODUCTION

## a. Aim

In many parts of tropical Asia two or more weaver species (Ploceinae), often apparently very closely related indeed, may be found side by side in a common, usually fairly homogeneous, environment. The question is at once posed as to how reproductive isolation is maintained between them and whether they compete with one another for certain biological necessities<sup>1</sup>. In recent years the ecology and behaviour of the commonest species, the Baya *Ploceus philippinus*, has been much studied (Ali 1931, Ali & Ambedkar 1956, 1957, Ambedkar 1958 and in preparation, Crook 1960c), and in 1959 a start was made on the other Indian species about which, apart from notes in Jerdon (1877), Oates (1883), Hume (1890), and Stuart Baker (1926, 1934), the standard works on Indian ornithology, and a short study by Spennemann (1926), very little was known. The area chosen for a comparative field study was the Kumaon tarai for this was known to be one of the localities where extensive sympatry of at least three species occurred.

During the visit the elusive Finn's Baya (*Ploceus megarhynchus* Hume), for long one of the mysteries of Indian ornithology, was rediscovered (Ali & Crook 1959) so that a total of four species was kept under observation throughout the same period. The enquiry was of necessity exploratory and consisted mainly in recording hitherto unknown details of the ecology and reproductive behaviour of *Ploceus manyar*, *P. benghalensis*, and *P. megarhynchus*, details which were quantified whenever possible. The observations on *P. megarhynchus* have already been published (Ali & Crook 1959) and the aim of this paper is, firstly to present the new data on *P. manyar* and *P. benghalensis* and, after comparisons with other Asian weavers, to review briefly the problems presented by the extensive sympatry of the group. As the paper goes to press the ecological work is being continued in Kumaon by Dr. Sálím Ali and Shri Vijaykumar Ambedkar.

## b. Study area—the Kumaon tarai

Below the Himalayan foothills the Kumaon area consists of a northern tract of forested country known as 'bhabar' and, to the south of this, a

<sup>1</sup> Modern theory assumes that species originate in the following way. The appearance of geographical barriers between local populations of a species prevents gene exchange between them. In isolation the adaptive differentiation of the separated populations continues leading to regional contrasts in physical, physiological, and behavioural characters which may prevent inter-breeding if and when an overlap in distribution occurs. If reproductive isolation is complete when this occurs the sibling populations are considered distinct species (Dobzhansky 1941, Huxley 1942, Mayr 1942, Lack 1944). The contrasts of particular importance in preventing inter-breeding are differences in courtship and mating behaviour and in habitat and food preferences (Hinde 1959). Furthermore the co-existence of sibling or closely related species in the same general environment depends also on the absence of ecological competition between them (Gause 1934, Crombie 1947).

flat largely treeless and often flooded stretch of grassland known as the 'tarai'. This type of country extends parallel to the bhabar for most of the length of the Himalayas north of the Ganges plain and reaches southwards to the river. The contrast between the forested bhabar and the swampy tarai depends on the fact that the drainage water from the Himalayas runs very deeply below the surface in bhabar, necessitating the construction of concrete surface runs from the hills and deep wells, whereas it emerges on the surface of the plain in the tarai and moves slowly along meandering streams and rivers down to the Ganges. In the monsoon season the tarai is subject to extensive flooding.

The four weaver species occur almost exclusively in the tarai, only the Common Baya having colonies in the agricultural lands in cleared bhabar. In the Rudrapur area of Nainital district colonies of all four species were observed; those of *P. philippinus* in bushy trees over ditches, streams, and rivers, *P. megarhynchus* mainly in *Salmalia* trees (Ali & Crook loc. cit.), *P. benghalensis* in grassland near flood pools and fish tanks, and *P. manyar* in reed and rush beds over swampy pools and in rushes over flood water. Mixed colonies of *P. benghalensis* and *P. manyar* occur both in rushes in swamps and in grass near flood pools, normally with one of the two species predominating. Thus, while differences in colony siting are apparent, the overall environment of the species is the same. All species are gregarious and it is probable that in winter, when the males lose the bright nuptial dress, the three smaller species flock together in search of food. *Ploceus megarhynchus*, much larger and with a massive bill, probably moves separately, and certainly exploits different food supplies although the degree of overlap in preferences remains unknown. All these birds are seed eaters, the smaller three in particular being granivores. In the monsoon season there is a fairly clear concentration of each species around their nesting colonies and this tends to promote some degree of ecological segregation. Females of *P. philippinus* have, however, been seen visiting colonies of both *P. benghalensis* and *P. manyar*, and the country is in general so homogeneous and the individual nesting habitats so interlaced that there is ample opportunity for interspecies communication. There are considerable differences in both nest form and site between the species. The Baya suspends its nests with long tubular entrances from the twigs of trees and bushes. *P. benghalensis* fixes its tubed nest to a wad of rushes passing through the fabric at the upper end of the structure. *P. manyar* builds a similar nest supported by the long leaves of rushes (*Typha*), which are often bent down and woven into the structure for the purpose. *P. megarhynchus* usually places its vast globular nest, with an entrance at the side near the top, in the terminal twigs of tree-tops but sometimes among reeds (*Phragmites*) standing in water.

## c. Field methods

The party consisted of Dr. Sálím Ali, Mrs. Eirene Harvalias Crook, the author and, for much of the time, Shri S. S. Bahadur, Wild Life Warden, Western Circle, U.P. We began work on July 10th 1959 and left the area on August 8th. Dr. Sálím Ali had to leave on July 23rd by which time the pattern of investigation had been well established. The original base of operations was Fatehpur (an excellent rest-house some 10 miles from Haldwani) and from here preliminary surveys were made. The later more detailed study, particularly of behaviour, was based on the Forest Rest House at Lalkua. The country was toured by car with additional trips into the forests on elephant back arranged by Shri Bahadur.

The colonies were studied from very close quarters, and the detailed movements of the birds observed with  $\times 8$  binoculars and when necessary with a  $\times 21$  telescope. The data recorded in the diagrams were taken down directly on tape using an EMI field tape recorder.

## II. NEW OBSERVATIONS ON TWO WEAVER SPECIES IN INDIA

a. *Ploceus benghalensis*

*Geographical distribution.* The species, of which only the nominate race has been described, is restricted to the northern regions of the Indian sub-continent from the East Punjab and Sind to eastern Assam, Sylhet, and Manipur. In western India it is found as far south as Baroda and there is a record from near Bombay (Hume 1890), but it is most common in the flat low-lying country of Bengal, Bihar, and the Ganges plain. It has not been seen in Burma. In most of its range it is local and capricious (Stuart Baker 1926).

*Ecology.* *Ploceus benghalensis* is essentially a bird of the plains and lower hills though it has been recorded breeding in a tea estate at 4000 feet (Baker 1926). Its common habitat is open country, grass covered and liable to monsoon flooding. The breeding colonies are placed in elephant grass or 'moonj' (*Saccharum munja*), often close to or standing in flood water. The colony studied most closely in Kumaon was built in tall grass on a bank overlooking a fish culture tank, some of the nests leaning out over the water itself. All were easily approached along the bank by passing carefully through the high grass that hid the colony from view on the landward side. On July 21st 1959, there were eight territories each with several nests, but later the number increased. At another colony there were seven nests in a patch of moonj reeds standing in a shallow pool. At a further colony some birds were nesting in rushes and grasses over water in association with *P. manyar*. Two



records from Bengal describe nests in low bushes over water on river or stream banks.

*Nests, sex ratio in the colony, eggs and clutch size.* The nests are finely woven unlined structures extremely similar to those of *P. philippinus* (Ali 1931, Ali & Ambedkar 1957, Crook 1960c). The fabric is identical except that it is not thickened to so great an extent by repetitive weaving. The structures are attached to upright grass stems woven tightly together by much stitching and entwining to form the wad base of the nest. The top of the nest is flat or dome-like, unlike the long thin supporting 'neck' of the Baya's structure. The male alone weaves and the entrance tubes may vary greatly in length, many being over a foot long. The nests are grouped into twos and threes at different stages of construction and each group is the work of a single male. When first observed (July 21st), the colony consisted of eight territories containing helmet stage nests, completed nests, and several ruined nests some partially constructed. All the old ruins had been abandoned and presumably represented an earlier attempt at breeding during one of the brief rainy spells that precede the monsoon proper. By July 25th each territory held several new structures many only a foot apart. While males were interested primarily in the latest nest they also maintained the earlier structures by 'titivating' them and, while primarily courting females near the latest structure, they also welcomed with greeting postures females already established. Polygamy was confirmed; several males having two nests occupied by females in their respective territories. As in the Common Baya the number of nests available for occupation is greater than the number occupied, and the number of females to a male perhaps varies from individual to individual and from year to year.

The eggs were white and their measures all fell within the range given by Stuart Baker (1926). Of 21 clutches examined in Kumaon in 1959 4 were c/5, 2—c/4, 12—c/3, 2—c/2, and one c/1. The mean thus is 3.25 eggs per clutch for the sample.

*Territorial Behaviour.* Three types of territorial defence were observed: supplanting attacks, head forward threats, and singing. Males move about the colonies outside their own territories a great deal particularly when following prospecting females, which fly from one territory to another on their visits. As soon as a territorial boundary is infringed the owner supplants the intruder and chases it away. Sometimes supplants lead to brief aerial combats. When two males are near one another between their respective nest groups 'head forward threats' occur. The birds flick their wings, turn towards one another with lowered heads and beaks pointing at the opponent, and hop about eyeing one another. These encounters are, however, brief and do not culminate

in protracted 'threatening matches', 'aggressive dances', or 'song bowing' encounters such as have been described for some African ploceines (Crook 1959, 1962, in press). Female intruders are usually courted, but may be threatened or supplanted, particularly if another male intrudes at the same time. The males frequently perch upright on grass stems near their nests and sing. The song is however so soft that it is almost inaudible to the human observer only a few yards away.

*Courtship.* The male *P. benghalensis* leave the dry season flocks before the females and establish nests and territories in the colony. They continue to forage and to roost with the females, and retain intact the flocking responses of the breeding season. There is evidence to suggest that, as for *P. philippinus* in the Bombay-Poona area, several false starts are made at breeding as soon as the rain falls at the onset of the monsoon. Breeding activity slows down and stops if the rainfall is not maintained, and only develops fully when the rains are well under way. Thus half constructed nests and abortive courtships are seen at a few localities where, a few days later, the nests are abandoned. Later still, renewed activity at the same spot culminates in breeding.

At the start of breeding the males keep strictly to their territories, building nests and supplanting intruding neighbours. The females fly into the colony, usually singly but occasionally in small groups, and proceed to hop through the territories and to approach the various nests. Should the male be absent a female will alight in his nest, examine it, titivate upon it, and then hop on into the next territory. As soon as a male observes an approaching female he leaves his nest and flies towards her, often leaving his territory, alights close beside her, and gives an intense wing beating display during which he moves along the grass stem towards her. Most of these displays occur on tall grass stems overhanging water which usually bend to a horizontal position under the weight of the performing birds (Fig. 1). The posture of the male in this 'Upright Wings Beating Display' (UWBD) has the following components:

- i. Wings beaten vigorously (mean speed 10 beats in 1.7 seconds  $n=21$ , Table I) fully elevated and extended above the back up to about 10 degrees from the dorso-ventral line of the body.
- ii. Body plumage sleeked except for some fluffing of the nape feathers.
- iii. Body crouched, oriented towards female.
- iv. Tail straight, rarely raised, often fanned.
- v. Beak turned down vertically so that the yellow crown faces the female.
- vi. Song.



The female crouches, somewhat sleeked but otherwise appearing unconcerned, until the male is very close to her. She then either hops a short distance away, flies a short distance, or pecks fiercely at her suitor. The latter may pause a moment before commencing his display again. If the female has flown some distance the male flutters after her, and, unless chased off by some territory owner upon whose defended area he has trespassed, again begins the wing-beating approach. This sequence is often repeated several times before the female flies out of the colony with the male in swift pursuit. They may fly for more than a hundred metres from the colony but eventually the female lands. The male alights near her and, on some occasions at least, again approaches her in display. Sometimes, however, he tires of the chase, alights some distance from the female, and then returns alone to his nest. The female is, however, clearly attracted by her pursuer for, commonly, as the male begins his return flight, she, without having landed, turns in flight and follows him swiftly to his nest where the familiar approach sequence is again performed. Sometimes during the return flight, if the female wavers, the male will turn again and start to chase her until she swings around once more and follows him to his territory. After several such chases the male often wing-quivers intensely in the presence of the female who now repeatedly hops on to the developing 'initial ring' (Skead 1947) of the nest. Often, after a bout of wing-beating approaches and mutual hopping about in the territory, the female goes to the nest and the male rushes to the nest entrance and performs an intense Upright Wings



Fig. 2. Upright Wings Rigid Display of *Ploceus benghalensis*. Wings outstretched at side of body in the plane of the back and held motionless. Tail extremely fanned. Bird facing female in or near nest.



Beating Display just outside. At moments of high intensity the wing-beating changes to 'wings rigid', recalling similar changes in the composition of the Advertisement displays of *P. cucullatus* and *P. philippinus* (Crook 1960c, and in press).

The 'Upright Wings Rigid Display' (UWRD) has the following composition :

- i. Wings fully spread and stretched out to full extent on either side of the body (at 90 degrees to the dorso-ventral line). They are quite still and have an appearance of rigidity.
- ii. Body plumage sleeked.
- iii. Body not crouched, bird usually hopping about.
- iv. Tail widely fanned and straight.
- v. Beak not turned down, usually oriented to female, but the head is not retracted into shoulders as in preparatory movements of lunging.

As the female leaves the nest the male commonly hops about the territory in this posture with her.

The female solicits the male either in the nest entrance or in the grasses below the nest. Her posture is a simple crouching accompanied by tail vibration in the vertical plane and wing-quivering. The male normally mounts at once. Frequently, however, in the course of these sequences the female attacks the male, particularly after he has made a close approach in the Upright Wings Beating Display posture. No pseudo-female solicitation has been recorded for the male.

A total of 71 courtship sequences were closely observed and recorded in detail on tape. These are presented in Diagram A which thus summarises the data and shows the frequency with which the various responses occurred. Altogether only 11.2% of all sequences included copulations or attempted copulations, whereas 32.3% included aggression from one sex or the other. In one case only did the male succeed in copulating when the female had previously lunged at him in the same sequence. Normally, only those sequences in which neither sex showed aggression ended in copulation. Most of the attacks were made on the male by the female (18/23 of sequences containing aggression) usually following the close approach of the former. Only 6 actual attacks on females by males were seen. Copulation normally followed intense wing-quivering which in all weavers indicates a strong tendency to respond sexually (Crook 1960b, c, and in press). In only 2/8 copulations did the response follow the Upright Wings Beating Display directly without an interim period of wing-quivering usually performed mutually. There was one anomalous response in which the male both sang at the female and wing-quivered to her. These data may be compared with those of *P. manyar* in Diagrams B and C and those of *P. philippinus* in Crook 1960c (Table V).

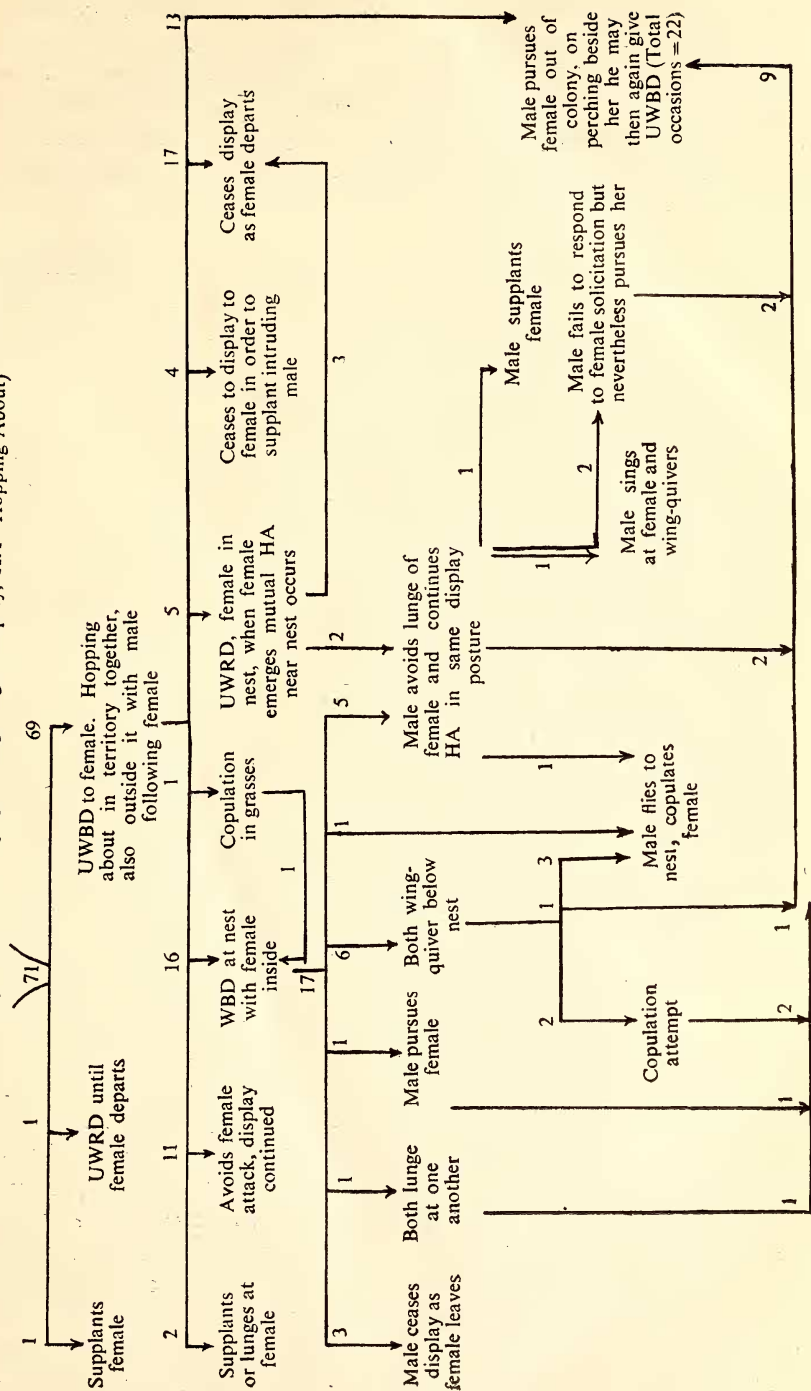
**Vocalisation.** Soft *chit chit* calls are given by birds flying into the colony. These appear to help in the orientation of the female to the male during the return flight to the nest. The soft, barely audible song *tsi tsi tsisik tsisik tsik tsik* 'like the chirp of a cricket or the subdued short squeaks of an unholed bicycle wheel' (Sâlim Ali, in litt.) is given during the UWB approaches to the female and also by males sitting solitarily within their territories. The extreme softness of the song, an anomaly among Ploceines, correlates with its utterance from a mere inch or so from the female to which it is given. The function appears to be courtship rather than advertisement (cf. *P. manyar*). In the alert 'song posture' when the male sings solitarily in his small territory there may be some advertisement significance for the neighbouring males close by. It is clear, however, that the contrast in loudness of song between this species and *P. philippinus* and *manyar* is due to its production at close quarters to the female [cf. Estrildid song (Hall 1962)].

#### b. *Ploceus manyar*

**Geographical distribution.** Three races of *P. manyar* are accepted at the present time. The nominate, *manyar*, extends throughout the islands of Java, Bali, and Bawean, *P. m. peguensis* occurs from Annam, Yunnan, Siam, Burma, and Assam into the Ganges Valley; while *P. m. striatus* (with which the former race *flavipes* is now merged) is found from NW. India through S. India to Ceylon. The distribution of the species is thus not only as great as that of the Common Baya, *P. philippinus*, but regional differentiation into races has similarly occurred. The range of the two races in northern India overlaps that of *P. benghalensis* the two species being, so far as is known, entirely sympatric within the range of the latter.

**Ecology.** *Ploceus manyar* inhabits flat swampy and rain-flooded lands in India and SE. Asia. In north India it shows a preference for swampy areas covered by rushes or reeds over standing water and colonies are normally so situated. In this it contrasts with *P. benghalensis* in the same area which tends to occupy grassland alongside flood water. *P. manyar* is locally distributed in most of peninsular India and Burma being limited to sizeable areas of swamp country. In the Ganges Valley and in Bengal colonies of some 40-50 pairs are usual, but in Sind and Punjab, where suitable tracts of reed-covered swamp are more restricted, it often breeds in very large colonies and Hume once found about 100 nests on a small bulrush island not twenty yards in diameter. Occasionally the species has been seen breeding in thorny bushes overhanging water (Hume 1890). Spennemann (1926) and Delacour (1947) write that in Java the nominate race nests in large colonies in bushes, trees, or palms, often near houses and usually over water, and it is common

DIAGRAM A. Behaviour sequences of male *Ploceus benghalensis* on the appearance of females in or near the territories. Total number of sequences observed 71. (UWBD—Upright Wing Beating Display, UWRD—Upright Wings Rigid Display, HA—Hopping About)



in a variety of terrain including reed beds, open grassy country, rice fields, and lowland gardens.

In Kumaon, colonies were situated in reeds or rushes over muddy pools in the tarai grassland, all in close proximity to colonies of *P. benghalensis*, *P. philippinus*, and *P. megarhynchus*. The colonies varied in size from 3-4 nests up to about 30. Three particular sites were watched during the visit.

*Nests, sex ratio in the colony, eggs and clutch size.* The nests of *P. manyar* are normally suspended from the tips of rushes or reeds usually bent down and incorporated into the wall of the structure (Fig. 4). The nests are 2-3 yards apart, at the closest one yard and in the most dispersed colonies about 6 yards. The structures are more coarsely woven than the nests of either *P. benghalensis* or *P. philippinus* and the top of the nest is rounded and not extended into flanges of weaving along the supporting reeds. The coarseness of the fabric is due to the use of strips of greater width for building than in the other two species. The tubular nest entrance is rarely developed much beyond the level of the bottom of the egg chamber floor in Kumaon, but in Java Delacour (1947) states that long tubes are made. This correlates evidently with siting in trees there.

The species is commonly monogamous. In one colony in Kumaon in 1959, groups of 5 and 3 nests respectively were closely observed and each nest was found to belong to a single male. This condition remained unchanged throughout the period of observation. In a large colony of 30 nests male *manyar* were never observed to visit more than a single structure except during occasional attempts to steal material. In no case was a male observed constructing a series of nests in the manner of *P. benghalensis* or *P. philippinus* in the same area. In addition in two nests males were seen incubating, an activity not recorded from polygamous male weavers and, in a mixed colony with *P. benghalensis*, males of the latter species continued courting and chasing females long after the male *manyar* had ceased to do so—although the nests of both species had been established at the same period. There are suggestions, however, that sometimes the species may breed polygamously. Thus, although Spennemann (1926) described monogamy in Java, Delacour (1947) says the species is polygamous there. In addition Sâlim Ali (personal communication) saw a single male with three nests at different stages all being maintained at once at Shamshabad in the Deccan in 1952, and in Kumaon he recorded two cases of males building a couple of nests each with courtship occurring at both structures.

The eggs are white. Some measurements exceed those of Stuart Baker (1926) made in south India (maximum length 21.6 mm., minimum 19.2, maximum breadth 15.1, minimum 13.1). The maximum length of



Kumaon sample of 16 eggs was 22.6 mm. with a minimum of 20.2, maximum breadth 15.5 with minimum 14 mm.

Of 7 clutches examined in Kumaon in 1959 1 was c/4, 4—c/3, 2—c/2, and none c/1. Ali (in litt.) in Travancore in 1933 recorded 1—c/3, 3—c/2, and 1—c/1. From these 12 clutches therefore the mean clutch size for the species is 2.85 eggs. Further figures may substantiate the slightly larger clutch size from the more northern population.

*Territorial behaviour.* The only aggressive behaviour observed between the males was an occasional supplant easily dodged by the offender. Trespassers over territorial boundaries were treated in this way but, compared with *P. benghalensis*, there was much less territorial infringement and this correlated with the different mode of pair formation of the latter in which the males fly out at females, and thereby enter other territories, much more frequently.

The males further advertise their territories by a loud and remarkably attractive song given when sitting solitarily on a conspicuous perch near or on the nest. This song undoubtedly emphasises territorial claims. Further, when females begin to arrive, the males perform Upright Wing Beating Displays near their nests often in social facilitation with one another. These mass performances undoubtedly make clear the position of defended areas to other males as well as the sites of potential nests to females.

*Courtship.* As in other Ploceines the males leave the flocks before the females and establish nests in territories in their colony sites. Flocking responses likewise are retained away from the colony itself. As soon as the nest sites are established the males respond to the arrival of other individuals, male or female, with dramatic Upright Wing Beating Displays. These are, moreover, given at the nests and do not follow a flight towards the female during her approach as in *P. benghalensis*. Approaching birds can be heard for a considerable distance and emit loud *chirt chirt chirt* calls continuously over a distance of at least 100 yards as they fly into the colony. This appears to alert the colony and coincides with the start of display by some of the males, display rapidly taken up by others through social facilitation. As soon as the females enter the colony they pass rapidly to the nests or territories of displaying males. The Upright Wing Beating Display, performed either on the nest or, more frequently, on rushes near it, has the following composition :

- i. Wings fully raised above the back at about 45 degrees to the dorso-ventral line of the body and beaten vigorously (mean speed 10 beats in 2 seconds,  $n=7$ , Table I).
- ii. Body plumage normal, not markedly sleeked.

- iii. Body upright, usually oriented to approaching birds or the female.
- iv. Tail straight, sometimes a little fanned.
- v. Beak neither turned down over chest nor pointed at female aggressively.
- vi. The bird calls *tre tre cherrer cherrer* repeatedly when performing in unison with other males, but in courtship to the female he sings a slightly curtailed version of the song.

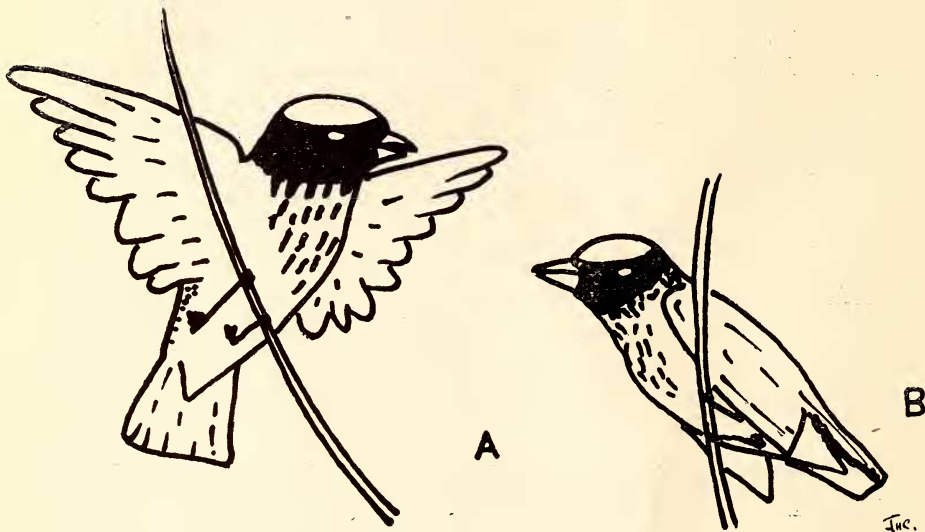


Fig. 3. A. Upright Wings Beating Display of male *Ploceus manyar*. B. Wing quivering of male *Ploceus manyar* to female in or near nest.

If a female enters the colony unnoticed she slips quietly into the territory of her choice, where the male greets her by going to the nest structure and performing the Upright Wings Beating Display. Often, however, the male supplants the female and chases her out of the colony. In the territory the female moves about into and around the nest in a 'sleeked' nervous posture while the male hops about in the display posture frequently singing, especially when she has entered the nest. Sometimes the male's display assumes the form of an Upright Wings Rigid posture with the wings held out on either side at about 90 degrees to the dorso-ventral line and quite still and rigid. He then sings loudly to the female who is usually in or emerging from the nest. When the female leaves the territory the male pursues her well beyond the colony following her flight manoeuvres closely. When she alights he comes down near her and quivers his wings in continued courtship after which he leads her back in swift flight to his territory turning to follow her at

once should she diverge from the flight line. On arrival he at once goes to his nest, perches in the initial ring, and, as the female arrives in the

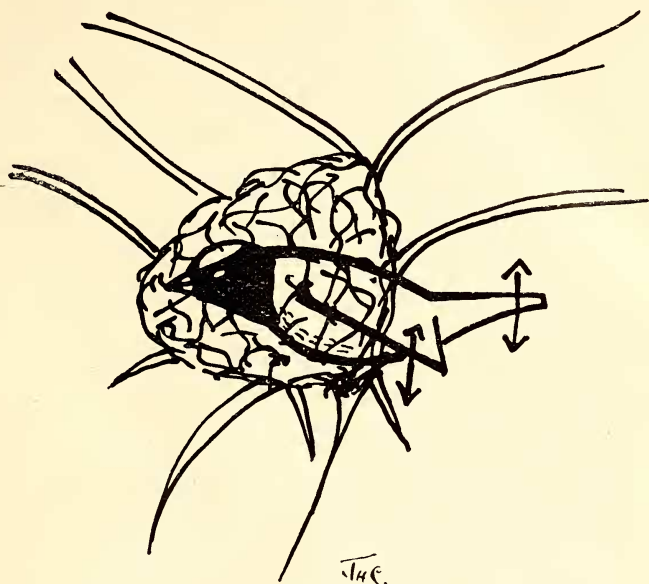


Fig. 4. Male *Ploceus manyar* giving pseudo-female solicitation in nest entrance of fresh incompleted structure.

territory behind him, he gives an intense 'pseudo-female solicitation' display with body crouched, wings drooped and tremored, and tail tremoring at high speed in the vertical plane (Fig. 4). The female then hops into the nest, the male emerges and usually attempts to mount her. At this she frequently flees and a further long chase follows until both return again calling the loud *chirt chirt* approach cry as they come in. When the female is receptive she solicits copulation, often as soon as she has arrived at the nest, in a crouched posture with quivering wings. Copulation occurs in the nest entrance or in vegetation near or below the nest.

During pursuit flights several males may join in the chase and, in general, competition between males for females is very considerable. Males sometimes zip into another's territory and attempt a stolen copulation as soon as the rightful male dismounts—a particularly fine piece of timing it would appear. Dr. Ali has also seen neighbouring males copulating, apparently successfully, with a single female during her visit to the colony.

In Diagram B, 19 sequences of early courtship during the first approaches of females to territories are shown. These are marked by displays near the nest and, if the female is receptive, attempts at copulation. In Diagram C, 26 later sequences depicting events following sex

chases away from the colony are shown. Here the male performs pseudo-female solicitation and attempts copulation when the female has perched in the nest entrance. In 5 sequences (heading B) he sang aggressively at the female after which she usually fled. If the female leaves the nest the male usually returns to it again and performs further pseudo-solicitation. 10/16 copulations in Diagram C occurred in the nest entrance, others below the nest in the reeds. Copulations in Diagram B likewise occurred in the nest ring. Only 29% of all sequences contained marked aggression while 47.1% ended in copulatory behaviour (Table IV). It is concluded that in courtship the species is much less aggressive than *P. benghalensis*. There are no records of female *P. manyar* attacking males and this clearly correlates with the absence of Wing Beating approaches. Finally pseudo-female solicitation indicates a conflict state in which sex and escape tendencies are active rather than the tendency to attack. This posture, common in *P. manyar*, has not been seen during the courtship of *P. benghalensis*.

*Vocalisation.* Vocalisations include: (i) the *chirt chirt* cries on approaching the colony, (ii) the *tre tre cherrer cherrer* calls in repetition during Wing Beating Display, and (iii) the song.

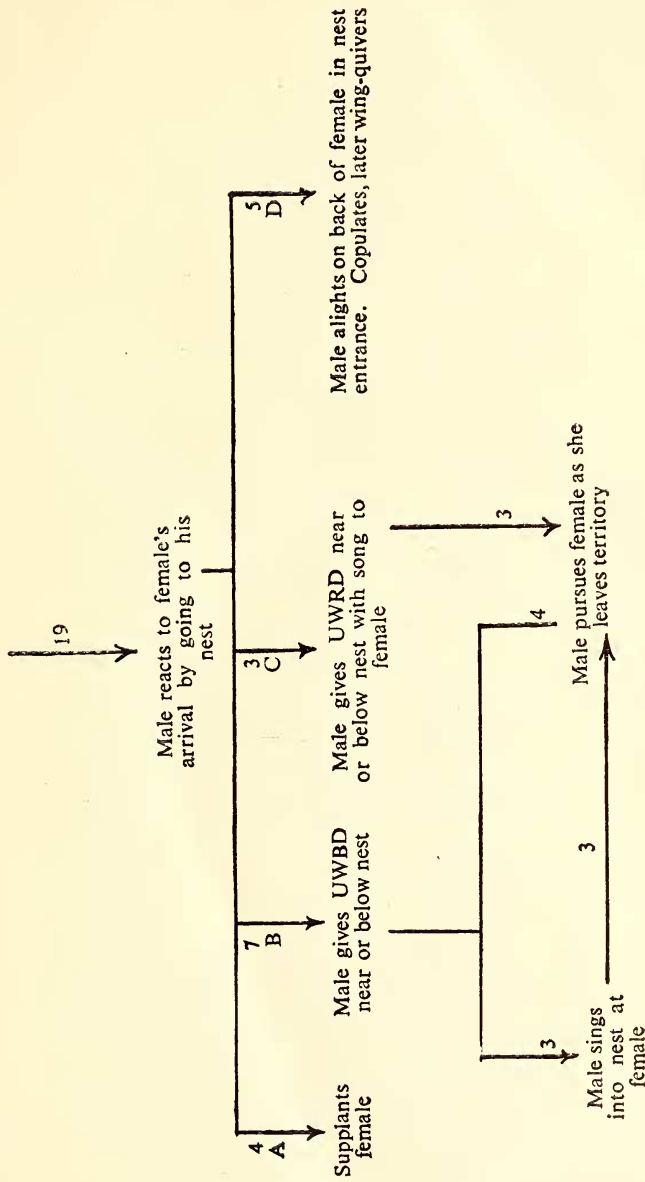
All these cries are louder and more emphatic than similar cries produced by *P. benghalensis*. The song is clearly aggressive though the tendency to attack is balanced by conflicting tendencies to retreat, remain near the nest, or to behave sexually, depending on context. Often, in company with the female, wing-quivering occurs with song indicating a strong sexual tendency. Even when song is clearly threatening, the female rarely abandons the territory completely but merely flies away and later returns with the male which has pursued her. Both the threatening and the chasing are probably highly stimulating to the female (Hinde 1953) and are an integral part of courtship although the initial chases are clearly more in the nature of supplanting attacks than sexual pursuits. Again copulatory behaviour commonly follows the return from a pursuit. The song which is charmingly musical, contains a long trill of about six notes (*tsi tsi* etc.) culminating in a long drawn wheeze. It is apparently not sung in choruses like the baya. It may be rendered *Tzrr we tsee tsee tsi tsi tser cheeze we*. It is often shorter when given to the female in courtship.

At times the males give a variety of chirring sounds particularly as a party arrives in the colony and each bird separates to his nest. The cry is apparently aggressive.

During mounting attempts the male flutters about after the female calling *chewe chewe chewe* repeatedly. When the female is soliciting she gives a very thin repeated piping call.

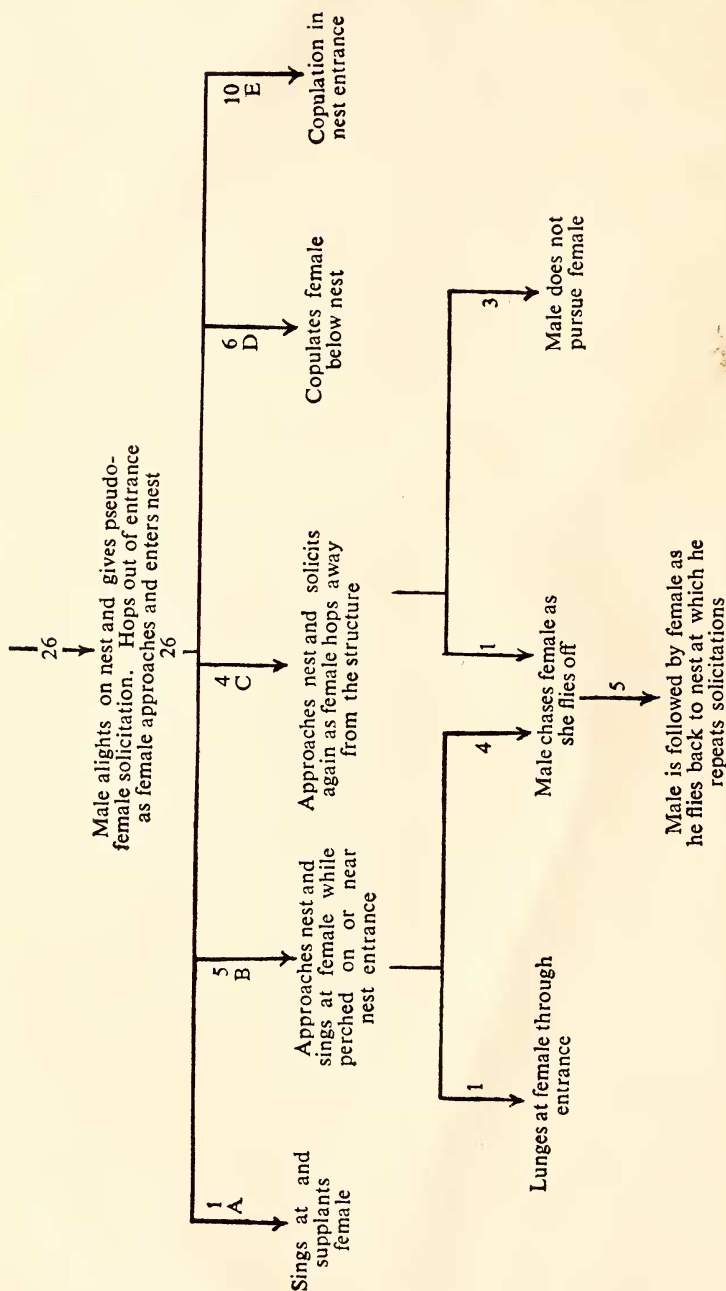


DIAGRAM B. Behaviour sequences of male *Ploceus manyar* in the territory following the arrival of a female on the nest either after her solitary entrance to the territory or after a pursuit flight. These sequences occur during the initial visits of females to the colony.



*Female responses.* In A, B, and C female remains sleeked, nervous. Finally she flies from the nest usually pursued by the male. Only in D does she solicit or permit mounting. Here the male does not display prior to an attempt at copulation.

DIAGRAM C. Behaviour sequences of male *Ploceus manyar* on arrival at the nest followed by the female. These sequences usually occur later in courtship than those shown in Diagram B.



*Female responses.* She follows the male into the territory, perches near nest and wing-quivers. She then approaches it and sits in entrance. If male performs A or B she flees but may return if male pursues and leads her back to the territory. After C she hops away and returns as male solicits; she then flies off. In cases D and E she solicits the male while he is likewise soliciting or wing-quivering. Copulation then follows.

### III. PROBLEMS OF PLOCEINE SYMPATRY IN ASIA, WITH PARTICULAR REFERENCE TO THE TARAI

Evaluation of the extent of competition and reproductive isolation between closely related species in the same area depends upon a detailed knowledge of the relevant ecological and behavioural variables. The existing information may be summarised under headings : (i) habitat selection, (ii) food selection, and (iii) mate selection. Differences in habitat and food preferences clearly reduce the likelihood of competition while in addition the habitat contrasts reduce the frequency with which species encounter one another in the breeding season and thus reduce the likelihood of attempted hybridisation. Contrasts in behaviour occurring in mate selection tend to inhibit pairing and prevent hybridisation.

Throughout the discussion it will be clear that differences in size, colour, beak proportions, and behaviour set *P. megarhynchus* apart from the other Indian weavers. Only *Ploceus hypoxanthus*, for which there is regrettably little information, appears to have some significant resemblances to *P. megarhynchus*. A general comparative summary of the relevant characteristics is provided in Tables II and III.

#### a. Habitat Selection

Differences in habitat preference are important in reducing ecological competition and the frequency of opportunities for hybridisation. In general *P. philippinus* is found in drier areas than either *P. benghalensis* or *P. manyar* and shows a strong preference for agricultural land rather than extensive grasslands or swamps. Furthermore, it requires trees, commonly in protective sites near water or around habitation, in which to construct its nests. Even in the arid Deccan the species appears locally wherever agriculture is permitted by the presence of seasonal streams or wells, over which the nests are commonly built. The nature of the bird's habitat suggests that prior to the establishment of wide-spread farming in India the bird was an inhabitant of damp 'savannah', nesting in colonies in trees over water. By contrast *P. manyar* requires extensive swampy areas and *P. benghalensis* the wet often seasonally flooded grasslands of the tarai. Both species place their nests low down in rushes (see further below) and grass respectively, and not in trees. At higher elevations only *P. philippinus* occurs ; for instance it is the only weaver in the Valley of Nepal.

In the tarai all three habitats, agricultural land with streams and a sprinkling of trees, patches of swamps, and extensive grass plains interdigitate tightly within the same general environment and the three species breed in adjacent, occasionally mixed (*P. manyar* and *P. benghalensis*), colonies in which, however, one species is normally in the majority. In

TABLE II  
SUMMARY OF GENERAL CHARACTERISTICS OF ASIAN WEAVERS

	<i>Ploceus philippinus</i>	<i>Ploceus manyar</i>	<i>Ploceus benghalensis</i>	<i>Ploceus megarhynchus</i>	<i>P. hypoxanthus</i>
Number of races	3	3	1	2	1
Habitat	Open country with agriculture and irrigation. Not in arid areas	Swamps, flood plains. Agricultural land etc. in Java	Grassy flood plains	Grassy flood plains with trees	Swamps, flood plains, Rangoon gardens
Colony site	Trees over water, vegetation over wells, palms, bungalow verandahs	Reeds, rushes, grass. Trees in Java	Grass beds, rushes	Tops of tall trees	Bushes in swamps etc.
Nest shape	Retort shape. Suspended or pendant	Retort shape. No neck. Short tube—longer in Java. Suspended	Retort shape. No neck. Suspended	Globular. Supported	Globular. Supported
Nest fabric, lining <sup>1</sup>	Fine weave. No lining. Mud blobs	Less fine weaving. No lining. Mud layer in some nests	Fine weave. No lining. Mud layer in some nests	Coarse weave. Lining. Mud blobs	Coarse weave. Mud etc.? Lining?
Pair formation	Inverted advertisement on nest precedes sex chasing	Upright WB near nest precedes sex chasing	Sex chasing with WB approach precedes visit to nest with female	Elaborate advertisement display postures. No sex chasing. Courtship entirely within territory	

Notes : (a) All Asian weavers are seed eaters, primarily granivorous, taking insects in the breeding season to feed young. Diet of *P. hypoxanthus* presumed the same. All are gregarious, colonial, sexually dimorphic and in the male seasonally dimorphic (female *megarhynchus* too apparently). All except perhaps Kumaon *manyar* population are polygamous.

(b) The southern races of *P. philippinus* and *P. manyar*, i.e. those of evergreen environments, have richer, darker coloration than those of the more arid monsoon areas in northern India. Abdulali (1961) describes the colour differences between *P. megarhynchus* races—the birds from Assam being more yellow on underparts etc.

<sup>1</sup> A very small amount of soft material is brought in by the female and placed on the floor of the egg chamber. Only in *P. megarhynchus* is the male known to line extensively.





Suspended nest of *Ploceus philippinus*



Nest of *Ploceus manyar* supported by rush blades (*Typha*)





Swampy grassfield nests of *Ploceus benghalensis*



Treetop nests of *Ploceus megarhynchus*

Photos : Dr. Salim Ali

peninsular India both *P. philippinus* and *P. manyar* are widely, though often locally, distributed but only where extensive swampy places are found in river valleys or coastal plains are the two species likely to occur together. Both are found again in Ceylon with the same habitat preferences.

In south-east Asia there is a more complex picture. In Burma and Thailand *P. philippinus* and *P. manyar* occupy habitats apparently identical to those in India. In Malaya only *P. philippinus* occurs and this is restricted to gaps in the prevailing forests and to farming areas. *P. hypoxanthus* also occurs with *P. philippinus* locally in Sumatra but the latter is the commoner. In Java, where *P. manyar* reappears, *P. philippinus* again appears the commoner in coastal areas. *P. manyar* now occupies a habitat around farmed areas and plantations nesting in trees and bushes (Spennemann 1926, Delacour 1947) and thereby differing considerably from other populations elsewhere. It is commonly found at higher elevations than *philippinus* though there seems to be considerable overlap in altitudinal range. Hoogerwerf (1947), in a survey of the birds of contrasting localities in Java, found it not only at sea-level but also up to 1500 feet in the area of Buitenzorg (Bandung) while he records *P. philippinus* only between sea-level and 800 feet. Delacour (loc. cit.) furthermore reports that the *manyar* nests in trees have long tubular entrances. Thus, in Java, far from being a swamp dweller, *P. manyar* seems to inhabit precisely the same niche as *P. philippinus* but primarily at a higher altitude. In addition Spennemann (loc. cit.) describes a difference in breeding season between the two species.

*P. megarhynchus* occurs in the tarai and usually nests in the tops of trees near canals or roads. It is sympatric with the other three Indian species and ranges widely though patchily over their breeding areas. In Burma and Thailand *P. hypoxanthus* occurs in swampy marshy areas often together with other species, and reappears apparently very locally (it seems to turn up only rarely in bird lists) in Sumatra and Java, again in similar habitats.

There are of course profound differences in the vegetation of India and south-east Asia, for whereas the former suffers a monsoon climate with an alternation of wet and dry seasons, in Malaya, Sumatra, Borneo, parts of Burma, and Thailand climatic conditions change little throughout the year and much of the land is covered with vast expanses of tropical rain forest in which Asian weavers are never found. In Java there is a monsoon season and a widespread deciduous forest, the rain forest being limited to favoured areas (Richards 1952). In India the plains of the tarai in winter are bare and dry and limited observations suggest that at this time the habitat preferences of the weavers break down entirely and the three smaller species then flock together in a mutual search for food. In addition they probably undergo migrations along the Ganges



Valley. It is thus likely that the habitat contrasts in the northern areas are only operative during the breeding season. In more constant climates (Ceylon, Burma, Sumatra) breeding and habitat differences are maintained for much of the year. In Java nothing seems to have been recorded of seasonal changes in bird activity.

#### b. Food Preferences

While it is generally agreed that the Asian Ploceines are all seed eaters to date no critical study of the subject has been made. In Poona *P. philippinus* takes a variety of seeds during the dry season mostly from the ground around farms and, in the breeding season, in addition to attacking ripening crops of jowar (*Sorghum*), bajra (*Pennisetum*), and maize (*Zea*), it brings insect food in the beak for the young in the nest. Similarly *P. megarhynchus* brings insects in the beak for its young but otherwise takes seeds. Nothing is known of its food outside the breeding season. The massive bills of both *P. megarhynchus* and *P. hypoxanthus* suggest food supplies differing from those of other weavers.

The beak sizes of *P. philippinus*, *P. manyar*, and *P. benghalensis* are similar and this, together with similarities in body size and gregarious habits, suggests that they take similar foods (Kear 1962). In order to evaluate more precisely the similarities in beak sizes, measurements were made on samples of British Museum material and analysed statistically (Appendix). The results show : 1) the beak lengths of *P. manyar*, *P. benghalensis*, and *P. philippinus* do not differ significantly. 2) The beak depths of the same three species do not differ significantly. 3) The beak lengths and depths of *P. hypoxanthus* differ significantly from those of the other three species. 4) A consistent difference in bill length was found between the sexes of each species, those of the males being the larger. This sex effect appears to be the same for all four species. 5) A similar sex effect was found in the beak depths but here the difference between the sexes for *P. benghalensis* was much greater than for the other three species (see Appendix). 6) The sex effect is presumably due to secondary sexual changes in the beak of the breeding male and is probably not sufficient to have any differential effect on the food taken by the two sexes. The larger beak of the male may be of survival value in nest building.

These facts suggest that, unless the responsiveness to food objects differs between the three species, they must take seeds and perhaps insects of the same size range whenever they feed together in the same area. In the breeding season such habitat contrasts as exist in Kumaon will tend to aggregate the species in differing areas so that local supplies will, to some extent at least, be utilised by different species. If, as seems possible, the flocks join up in winter then the conclusion that they take

the same food is inescapable. If this is so when the food supplies are insufficient to support the whole population competition between the individual members of the flock for the diminishing supply must occur. In such competition any individuals which through dominance or any other characteristic (such as faster 'follow up' responses ensuring quicker arrival at limited food supplies found by the group) have an advantage over their fellows will tend to survive at their expense and ultimately replace them throughout the area. The result of such a process has been expressed in Gause's Law (Gause 1934).

There are, however, certain conditions under which sympatric species in the same niche can maintain their numbers in a balanced population. Such conditions are those of food 'superabundance' (Lack 1954). Moreau (1948) has in fact suggested that competition between the species members of mixed flocks of weavers in Africa is prevented by the overwhelming quantity of grass seed in the savannah areas at the end of the rainy season and that the birds move from one rich food area to another as the supplies are exhausted. Alternatively, factors other than density-dependent mortality through food shortage may control the absolute and relative numbers of birds present (i.e. see Wynne Edwards 1959, Ripley 1959a). If this were so and the numbers maintained at such a level that food supplies were never limiting, clearly competition would not occur. In the Ganges Valley 'superabundance' of food is most likely at the start of the dry period but it seems improbable that this should outlast the season. Competition, it seems, must occur at some times and in some localities in every year, but its extent and duration remains an open problem. One method of study would be to weigh samples of natural populations throughout the dry season.

### c. Mate Selection

As all the weavers breed in the monsoon real possibilities of cross breeding exist in nature. Only in two cases are there differences in breeding season between sympatric species. In the Kumaon *P. megarhynchus* breeds earlier than *P. manyar*, *P. benghalensis* and *P. philippinus* though there is some overlap in timing. Similarly in Java Spennemann (1926) states that while *P. philippinus* starts breeding in early February *P. manyar* does not begin until middle or late March. As these two species are so similar in their habitat preferences in Java this contrast is likely to have considerable significance in preventing hybridisation.

Factors reducing the chances of interspecies mating in these weavers are contrasts in : (i) coloration, in particular the nuptial dress of the male, (ii) the sequence of events in courtship, (iii) the postures of advertisement and courtship display, their orientation and accompanying vocalisation, (iv) nest site, (v) nest form and fabric, and (vi) habitat. The relative importance of these factors is undetermined, but present



observations suggest that i-iv are of particular significance with other factors playing a contributory role. Mate selection, which is performed by the female, is probably a response to the summation of the effects of numerous mutually reinforcing stimuli from the male, his nest, and the context of the whole behaviour. If any factors have negative valence they will play the part of 'inhibitors' (Marshall 1959) the summation of which may prevent breeding.

i. *Coloration.* The coloration of male weavers is species-specific and minor contrasts also exist between the females. In parti-

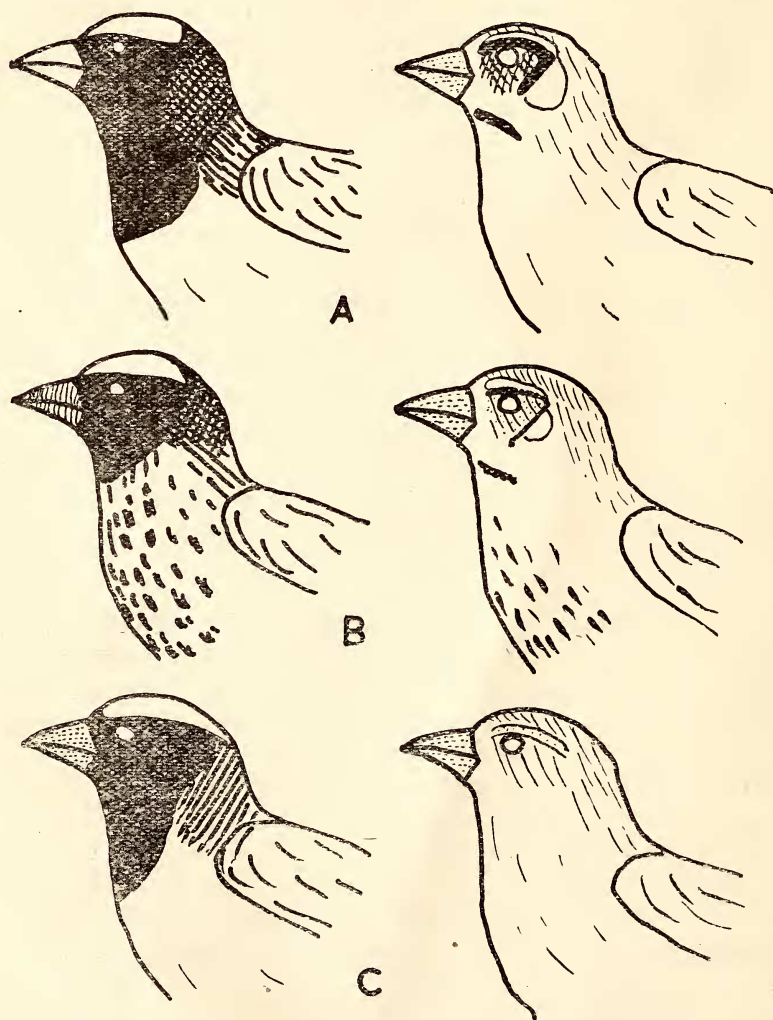


Fig. 5. Heads of male and female weavers. A. *Ploceus benghalensis*. B. *Ploceus manyar*. C. *Ploceus philippinus*.

## EXPLANATION TO FIGURE 5

MALES	A. <i>P. benghalensis</i>	B. <i>P. manyar</i>	C. <i>P. philippinus</i>
Beak	Blue	Black	Dark brown horn
Crown	Orange-yellow	Golden yellow	Golden yellow
Face	Black with dark brown nape	Black with brown striated nape	Black with brown nape
Breast	Black	Striated	Upper black ; lower yellow
Underparts	White	Striated ; white on belly	Yellow ; white on belly

NOTE : In the field male *P. manyar* often showed striated nape running up as a cleft for a short distance into yellow of crown. Yellow ends in straight line in *benghalensis*.

FEMALES	A. <i>P. benghalensis</i>	B. <i>P. manyar</i>	C. <i>P. philippinus</i>
Beak	All females have beak of horn brown colour.		
Superciliary stripe	Yellow above thick black line	Pale yellow above thin dark brown line	Pale fawn
Cheeks	Grey	Fawn	Dark fawn
Ear coverts	Large yellow patch behind black line	Small pale yellow patch behind brown line	Dark fawn ; no yellow
Chin	Yellowish white	White	White
Moustachial streak	Black	Dark brown	None
Breast	Pale fawn	Striated	Pale fawn

All the characters listed are those observed through  $\times 8$  binoculars in the field and found useful for identification of females in the colonies.

cular the yellow heads and bodies, including the rump, of both *P. megarhynchus* and *P. hypoxanthus* males set these species apart from the others. *P. philippinus*, *P. benghalensis*, and *P. manyar* are alike in colour patterning, the main contrasts being the black chest in *P. benghalensis*, streaked in *P. manyar*, and yellow in *P. philippinus*. Further, while the bills of breeding male *P. philippinus* and *P. manyar* are dark brown-black, those of *P. benghalensis* are pale blue (see details—Fig. 5).

ii. *Sequence of events in reproductive behaviour.* Here again the behaviour of *P. megarhynchus* contrasts sharply with the other Indian species ; in particular courtship is restricted to the territory and no

sexual chasing occurs (Ali & Crook 1959). Nothing is known of the courtship of *P. hypoxanthus*.

In general the events and postures in the reproductive behaviour of *P. philippinus*, *P. manyar*, and *P. benghalensis* are remarkably alike. There are however important contrasts in the sequence in which these events occur and in the precise context in which the Wing Beating Displays are given. This contrast in context also involves a shift in the function of the display. In Table III the sequences of events for the three species are summarised. Thus in *P. philippinus* the timing of events goes : (a) Nest Advertisement (i.e. invitation) and acceptance ; (b) Courtship in the territory with sex chasing outside it ; (c) Mating in the territory. In *P. manyar* it is : (a) Advertisement Display in the territory ; (b) Sex chasing and courtship, the latter both within and without the territory ; (c) Nest invitation by pseudo-female solicitation by the male, and mating. In *P. benghalensis* : (a) Courtship approaches to female with WBD and sex chasing ; (b) Flight to the nest, female following and entering with male WBD outside ; (c) Nest acceptance and mating. Thus whereas in *P. philippinus* and *P. manyar* advertisement precedes courtship, in *P. benghalensis* courtship comes first and nest visiting second. In all three species, however, unlike *P. megarhynchus*, sex chasing is an important element in courtship.

iii. *The postures of Advertisement and Courtship and contrasts in motivation.* The main contrasts here are :

(a) The WBDs of *P. philippinus* are usually inverted below the nest while those of *P. manyar* are upright and given in the territory usually near the nest rather than upon it. The WBD of *P. benghalensis* is given without reference to the nest and is exclusively oriented to the female. Thus, while the displays of the first two species have advertisement function in attracting females to nest and territory, that of *P. benghalensis* is essentially a courtship posture. The extreme similarity of these displays indicates their homology.

The compositions of the ritualised WBDs are remarkably alike. The wing beating speeds differ but little (Table I) and tail elevation varies only in the greater frequency of depression in *P. philippinus*. There are, however, differences in wing arc, the elevation of *P. manyar* and *P. benghalensis* being greater than that of *P. philippinus*. Again while the beaks of *P. benghalensis* and *P. philippinus* are normally turned down during display (Fig. 1) that of *P. manyar* (Fig. 3) is not. *P. benghalensis* gives a short soft song during display while *P. manyar* gives a curtailed song phrase, and *P. philippinus* a special cry (Crook 1960c). All these contrasts probably originated through differential sexual selection of displays in isolated populations, but the tail and beak differences originally probably expressed motivational contrasts in courtship prior to posture ritualisa-

TABLE III  
SEQUENCES OF EVENTS IN THE REPRODUCTIVE BEHAVIOUR OF *PLOCEUS PHILIPPINUS*, *P. MANYAR*, AND *P. BENGHALENSIS*

<i>Ploceus philippinus</i>	<i>Ploceus manyar</i>	<i>Ploceus benghalensis</i>
I. Females approach established colonies.	I. Females approach established colonies.	I. Females approach established colonies.
II. Males give inverted WBD in Advertisement on nest with a special cry. Social facilitation between males occurs.	II. Males give UWBD on rushes etc. in their territories as an Advertisement Display. Social facilitation sometimes occurs.	II. Males approach females often outside the territory and give UWBD with depressed beak and song. This is the initial courtship posture. No social facilitation between males.
III. Females enter nests.	III. Female enters territory and may go to the nest. Finally flees with male in a sex-chase.	III. Female follows male to territory and either goes to nest or flies away again. Sex-chases follow.
IV. Male gives a WR posture and bows with a song into the nest. If female flees nest he pursues her in sex-chase, if she stays in territory courtship occurs.	IV. Female follows returning male to territory. Male performs pseudo-female solicitation in the nest entrance.	IV. Female follows male to territory and goes to the nest. Male displays UWBD or often UWRD outside nest entrance.
V. Mutual adjustments, male chases female aggressively from territory many times. Sex-chases lead to renewed courtship.	V. Female enters nest and male at once attempts copulation. Female may flee but commonly accepts.	V. Mutual adjustments. Female commonly attacks the male as he approaches her in display. Sex-chase often repeated.
VI. Female solicits in nest ring. Copulation.	VI. Copulations in nest entrance etc.	VI. Copulation in nest entrance etc.



tion. Thus tail depression, otherwise common in threat, suggests that prior to ritualisation the tendency to attack was strong during the relevant phase of *P. philippinus* courtship. Similarly beak depression suggests a tendency to escape in conflict with attack (Crook in press, in preparation). Such contrasts are supported by an analysis of the motivation of contemporary unritualised posturings in the courtship of the three species.

(b) The 'pseudo-female solicitation' posture occurs in *P. philippinus* (Crook 1960c) and in *P. manyar* but not in *P. benghalensis*. In *P. manyar* it is most marked and plays a special role in enticing the female to the nest and in initiating copulatory behaviour (Fig. 4).

Contrasts in behaviour sequences and postures express differences in motivation. Analysis is based on the methods of Tinbergen 1959, Hinde 1953, 1955, 1956, Morris 1956, Andrew 1961 and follows analyses of other Ploceinae (Crook 1962 etc.) in which the rationale is given in detail. In brief, the reproductive behaviour of the weavers is determined by the interaction of attack, escape, and sexual responses in conflict. The relative strengths of these tendencies in courtship vary between related species and produce contrasting behaviour patterns. In addition the strength of attachment to nest during courtship varies between the species. The number of sequences containing attack (and threat) is particularly high in *P. philippinus*, high in *P. benghalensis*, but low in *P. manyar* (see Table IV). In correlation with this a particularly high percentage of sequences ends in copulatory behaviour in *P. manyar* while *P. philippinus* and *P. benghalensis* show low percentages. In the latter species this is probably due to the fact that 18/23 recorded sequences containing aggression involved attacks by females on approaching males. The giving of aggressive responses in a sequence clearly reduces greatly the chance of a copulation in that visit, aggression inhibiting sexual behaviour. By contrast in *P. manyar* the high rate of copulatory activity correlates with a high frequency of male behaviour patterns expressing sex and escape tendencies in conflict (the 'pseudo-female postures' see Morris 1952, Hinde 1955, 1956, Crook 1960b).

These comparisons suggest : (i) The threshold for attack on females entering a territory is low throughout the early courtship of *P. philippinus* and is only gradually raised as the sexual tendency increases in strength during courtship. The tendency to remain at the nest is strong until the female has actually entered the structure after which chases occur. (ii) In *P. benghalensis* the male has a low threshold for sexual behaviour and the tendency to remain at the nest is weak. Thus on the approach of a female he flies out and approaches her. The nearer he gets the stronger becomes his tendency to escape. The female at first responds to these approaches, often within her individual distance, with attack. Only after many sequences does her threshold for attack rise as she begins to respond sexually to the male's approaches. (iii) The male *P. manyar*, shows



particularly strong tendencies to behave sexually and to flee from the approaching female. This is associated with relatively strong nest attachment and a high threshold for attack.

It follows that while aggressiveness inhibits the early expression of sexual behaviour in the sequences of *P. philippinus* and *P. benghalensis*, in the former case this is due to the male's tendency to attack approaching females near his nest, and in the latter to the female's aggressive response to the approach of courting males. In *P. manyar* courtship attempts by the male are frequently frustrated by the female's lack of responsiveness rather than by aggression by either sex.

To summarise: the displays and postures of the three species are homologous. The WBD clearly plays an important role in mate selection, and females probably react specifically to the posture composition (and coloration) and also to the display orientation. The major contrasts concern orientation—whether the display is given to the female away from or at the nest, and whether it is upright or inverted. Such contrasts undoubtedly enhance the likelihood of reproductive isolation, particularly since they are maintained when two species are breeding in mixed colonies (*P. manyar* and *P. benghalensis*) in the same habitat. Both the contrasts in behaviour sequences and in postures depend largely on differences in motivation between the species.

TABLE IV  
COMPARISON BETWEEN THE BEHAVIOUR SEQUENCES OF THREE ASIAN  
WEAVERS DURING PAIR FORMATION

Species	No. of sequences containing attack or threat upon sex partner	No. of sequences ending in copulation or attempted copulation	Other sequences ending inconclusively in the departure of the female	Total of sequences
<i>Ploceus manyar</i> (Diagrams B and C)	13 (28.8%)	21 (46.7%)	11 (24.4%)	45
<i>Ploceus benghalensis</i> (Diagram A)	23 (32.3%)	8 (11.2%)	40 (56.4%)	71
<i>Ploceus philippinus</i> (Schemes B and C in Crook 1960c)	31 (65.9%)	13 (27.6%)	3 (6.5%)	47

NOTES: (a) In *P. benghalensis* 18/23 aggressive sequences were initiated by the females as against 7/31 in *P. philippinus* and zero incidence of female attack on males in *P. manyar*. Other attack sequences were initiated by territorial males. Discussion in text.

(b) Statistics: An overall  $\chi^2$  test gives the significance of the differences between the proportions for the three species at the 0.001 level and similar tests, taking the species in pairs, give in each case significance at the same level. Real behaviour differences are thus considered established.

iv. *Nest site.* It is uncertain how far differences in nest site as such are of direct significance to the female. For instance in Kumaon *P. philippinus* females visit *P. manyar* colonies in reeds and hop about actually visiting their nests in the absence of the males. It seems probable also that female *P. manyar* and *P. benghalensis*, not easy to distinguish quickly in the field, may also visit each other's untenanted nests particularly in mixed colonies. No *P. manyar* or *P. benghalensis* females have been recorded in the tree sites of *P. philippinus*, however, and although *P. megarhynchus* often build nests (in Kumaon) in rushes they have not visited structures of *P. manyar* when perching in their colonies.

v. *Nest form and fabric.* The fact that female weavers spend much time examining and adjusting the fabric of the nests they visit suggests that differences in nest form and the manner of construction might inhibit acceptance of a nest not built by a male of the species. The globular structures of *P. megarhynchus* and *P. hypoxanthus* are of course quite different from those of the other species, and where *P. hypoxanthus* and *P. manyar* are sympatric this may be a factor preventing female interest in each other's colonies or nests. Nests of *P. benghalensis* and *P. philippinus* are particularly alike both in form and in the fineness of the materials used although mud is plastered more extensively in the interiors of some *P. benghalensis* nests than has ever been recorded for *P. philippinus*. *P. manyar* nests are rough, rather 'angular' balls made of coarser materials and have a shorter tube (in Kumaon), and mud is often plastered fairly extensively in the egg chamber. Nonetheless female *P. philippinus* visiting *P. manyar* colonies not only enter the nests but mandibulate the fabric extensively suggesting little appreciation of these differences. Spennemann (1926) considered nest construction important in pairing and showed that male *P. manyar* destroy nests not accepted by a courted female and build another in the same or a near-by site. Sálím Ali (1931) has also recorded the destruction of unaccepted nests by the male *P. philippinus*.

vi. *Breeding habitat.* Specific preferences for certain habitats undoubtedly play a major role in ensuring reproductive isolation. Where, however, the preferred habitats are dovetailed in an intricate fashion as in the Kumaon area, direct segregation of the species is very much reduced and the factor of less significance.

#### *Observed attempts at cross-mating*

So far no direct evidence for hybridisation between any Asian weaver species in the wild has been obtained, and in captivity there are only two records of possible hybrids between *P. manyar* and *P. philippinus* (Gray 1958). There are, however, some observations showing that male

*P. benghalensis* do occasionally chase and mount female *P. manyar* in mixed colonies. In a particular case recorded by Sálím Ali (in litt.) the female was already mated and in possession of a nest of its own species.

Such cases are probably due to the relative inability of males to distinguish quickly their own mates and females of their own species. Since, however, it is the female which ultimately chooses her mate and nest, and which therefore plays the fundamental role in mate selection (as in the American Grackles, Selander & Giller 1961), it follows that only observations showing females to have chosen mates and nest of a species other than their own can be considered evidence for hybridisation of any biological significance. No such cases have yet been recorded.

#### d. C o n c l u s i o n s

The above discussion allows the following conclusions regarding the extent of competition and the maintenance of reproductive isolation between sympatric Asian weavers.

#### C o m p e t i t i o n

(a) *Ploceus megarhynchus* probably has quite different food preferences from those of the smaller species in Kumaon. In SE. Asia *P. hypoxanthus*, probably also takes different food from the three smaller weavers.

(b) *P. philippinus*, *P. manyar*, and *P. benghalensis* probably take similar or identical foods and must compete for nourishment in environments where they are sympatric if food supplies are limiting. Differences in habitat preference in the breeding season and food 'superabundance' for at least part of the dry season probably reduce the extent of competition considerably. Exact measures are required. In Java contrasts in breeding season and altitudinal range between *P. philippinus* and *P. manyar*, the nest siting of which is identical there, have been noted.

#### R e p r o d u c t i v e i s o l a t i o n

(a) Differences between the species in six sets of variables influence to varying extents the likelihood of matings between the closely related species. Matings between *P. philippinus*, *P. manyar*, and *P. benghalensis* are possible, especially between the last two in north India and the first two in Java where ecological similarities are particularly apparent. In the latter case, however, contrasts particularly in the timing of the breeding season reduce the likelihood of hybridisation.

(b) Of the variables discussed, contrasts in the coloration of the males, in the sequences of events in courtship, in posture composition, and in song are likely to play a direct role in inhibiting cross-matings. Contrasts in the behavioural context, orientation, and form of the ritualised

Wing Beating Displays are probably especially significant as the latter function as signals in the initial communication between the sexes at the onset of pairing. The contrasts in orientation are particularly important and are closely linked with the differences in nest site. Differences in the conflict motivation shown by each species in the behaviour sequences are apparent, and might involve incompatibilities in any attempted hybridisation in addition to the effects described above.

(c) The close contiguity of breeding colonies of *P. manyar* and *P. benghalensis* allows males to attempt copulations with females of species other than their own. Females have, however, never been seen choosing mates and nests of another species.

These results suggest that some degree of competition may exist in India particularly between *P. manyar* and *P. benghalensis* and in Java between *P. manyar* and *P. philippinus* although in both cases this must occur only for limited periods and only in the few localities where extensive sympatry occurs. Inter-breeding between the species is prevented by a number of species-specific characters.

#### IV. THE EVOLUTION OF THE ASIAN WEAVERS

##### a. The African origin of the Asian weavers

The weavers (Ploceinae) are found throughout Africa and tropical Asia but not in the desert areas of the Sahara and the Middle-East. Most of the 95 species occur in Africa and only 5 are known in Asia. In Africa all biomes have weaver representatives: rain forest, montane forest, humid and dry savannah, lakeside, and grass. The Asian species, however, are restricted to savannah, grassland, and swampy country.

In spite of the absence of a fossil record a coherent evolutionary picture of a bird family can be built up from two sorts of evidence: firstly, a precise knowledge of comparative anatomy and behaviour together with an understanding of the functional significance of these characteristics in relation to species ecology, and, secondly, a knowledge of the ecological changes dependent upon climate, which have occurred within the geographical range of the group during the relevant period of time. While at present this latter type of evidence is meagre there is sufficient to construct an hypothesis which represents in outline the likely course of events. The picture will become clearer not only through further study of the birds themselves but through an improved understanding of the phyto-geographical changes in Asia since the Pliocene.

The following points suggest that the ancestors of the Asian weavers invaded Asia from Africa at a time, or at times, when a suitable tract of country connected the two continents.



(a) Prior to the Miocene unbroken evergreen forest is believed to have stretched from West Africa to eastern tropical Asia. As the weavers are not represented in the Asian forests they could not have been part of the widespread pan-Afro-Asian avifauna of that time. They must have invaded African evergreen forests after the biome had split.

(b) The great majority of weaver species occur in Africa which has been the main centre of radiation of the group.

(c) The weavers appear to have originated as savannah species and to have entered forest secondarily (Chapin 1923, Crook in preparation). Their spread northwards and eastwards into Asia was dependent upon the existence of a suitable tract of open country in those areas.

(d) The Asian weavers are few, all are open country birds of general similarity to African savannah species but showing signs of long isolation and parallel evolution. Typical African grassland weavers (i.e. *Euplectes* spp., *Quelea* spp., etc.) and insectivorous weavers (i.e. *Malimbus* spp., *Ploceus bicolor*, etc.) are not represented in Asia suggesting that only the most adaptable seed eating species of the genus *Ploceus* reached a latitude sufficiently northerly to turn the Arabian Gulf and spread into Asia.

The suggestion that Asian weavers came from a stock of savannah adaptation is supported by their nest structure. The tubed nests (retort shape B, Crook 1960a, and in preparation) of *P. philippinus*, *P. manyar*, and *P. benghalensis* are characteristic of weaver construction in trees when fine terminal twigs are used for suspension. In Africa such nests occur in both forest and savannah. In swamp, grass, or scrub, however, African weavers have globular nests supported from below rather than above. Now, in spite of major contrasts in nest site, *P. manyar* and *P. benghalensis* retain the same basic tubed nest as *P. philippinus*, and all are suspended from their upper parts. This indicates that the Asian grassland and swamp species are derived secondarily from a tree-nesting stock, to which *P. philippinus* is presumably very similar, and that in the absence of selection to the contrary they have retained the tubular entrance to the suspended nest. Only in *P. manyar* is there a noticeable shortening of the tube. Since there are no forest weavers in Asia the tree-dwelling ancestors must have lived in savannah.

The nests of *P. megarhynchus* and *P. hypoxanthus* are globular but, while that of the latter is only sited in bushes in swamps (etc.), the former places its nest both in a curious tree-top site (Ali & Crook 1959) and in reeds. This major contrast with the *P. philippinus* species group, taken together with other anomalous characteristics, suggests that *P. megarhynchus* and *P. hypoxanthus* come from a separate stock. The nest construction and siting suggest that these birds built globular nests in dense scrub or marsh in the manner of *Quelea quelea* (Morel, Morel & Bourliere 1957) in Africa today. Once in Asia, they became specialised to their particular sites and ways of life in different areas.



(e) As no Asian weaver lives in particularly arid areas, except where watercourses, wells, and agriculture provide tolerable conditions for *P. philippinus*, it can be assumed now that their ancestors belonged to the relatively humid African savannah contribution to the Indian avifauna rather than to the Somali-Arid element (Chapin 1923, Hussain 1958, cf. Ripley 1959a).

Only two Asian weavers are widespread over the whole area (*P. philippinus* and *P. manyar*), and only *P. philippinus* can be considered a very common bird. *P. benghalensis*, *P. megarhynchus* and *P. hypoxanthus* all have small ranges and those of the latter two species are much subdivided. This suggests that, while the weavers spread widely in Asia on their arrival and underwent adaptive radiation, obscuring any close relationship with African forms, later phyto-geographical changes brought about restrictions in range for all except the two species able to take active advantage of them (*P. philippinus* and *P. manyar*). Thus, while *P. benghalensis*, *P. megarhynchus*, and *P. hypoxanthus* are essentially relict populations, *P. manyar* and especially *P. philippinus* are dynamic and expanding stocks (see Darlington 1957).

Although a general similarity between the African and Asian weaver faunas persists, certain details of weaver life in Asia are peculiar to that area. These features are : (i) the development of colonial life in areas of short rainy seasons without reduction of courtship activity outside the territory (*P. megarhynchus* excepted) ; (ii) the development in *P. philippinus* of elaborate nest repair behaviour ; (iii) the use of mud in nest construction (*P. hypoxanthus* ?). These points refer particularly to *P. philippinus*, *P. manyar*, and *P. benghalensis* and are probably all correlated closely in relation to the survival value of the particular type of nest constructed by them. *P. philippinus* resembles closely many colonial species of relatively dry areas in Africa, but unlike them does not show reduction in the amount of sex chasing beyond the limits of the territory. In African species such as *P. cucullatus* the survival value of this limitation is held to be that it reduces the frequency of nest robbing attacks by neighbouring males by increasing the amount of time spent in active occupation of the territory. Nest robbing is known to delay nest completion appreciably and, in a short breeding season, this reduces the chances of a male acquiring a maximum number of females for his nests and of having young in them during the period of optimum food availability. Furthermore, females will only accept properly completed nest baskets with at least a fine floor to the egg chamber. In *philippinus*, by contrast, the male is often absent from his nest and sex chasing and nest robbing then occurs without hindrance. Any damage done is, however, repaired with a speed and agility not seen so far in tests on African species. In addition the male brings several strands of material to the nest on each visit and the method of construction is such that it encourages rapid

repair and constant fabric maintenance. Female *P. philippinus* accept nests in the 'Helmet stage' when the floor of the egg chamber is not yet finished. The males await acceptance before completing the structure. Furthermore, *P. philippinus* maintains the nest by constant attention throughout its occupation. These features of construction, together with the use of mud, appear originally to have been adaptations to rain-shedding, thereby keeping the young from chilling. Additionally they permit rapid nest repair thereby eliminating the necessity of a courtship restricted to the nest area (Crook in press). *P. benghalensis* and *P. manyar* have not yet been tested for their repair abilities. Some observations suggest that the constant padding of the fabric, typical of *P. philippinus*, is absent. The nest sites in thick vegetation with a reduced visibility between nests may entail a reduced frequency of nest robbing compared with the tree site and hence less need for repair. Furthermore, the nests may be better protected from rain. In conclusion the contrasts between *P. philippinus* and similar African species are interpreted as different adaptations to identical selection pressures occasioned by high seasonal rainfall and nest robbing by other males.

#### b. Dispersal and adaptive radiation

The dispersal of weavers through Asia depended upon the provision of suitable climatic and vegetational conditions. It is therefore essential to determine, so far as possible, the nature of the phyto-geographical changes that occurred within the relevant time period. Recent studies suggest that the age of the Oscines is very much less than had previously been suspected—their radiation probably occurring primarily in the Miocene (Darlington 1957). Furthermore, while Brodkorb (1960) puts the average longevity of pleistocene birds at about  $\frac{1}{2}$  million years and the top longevity at one million, Moreau (in press) points out that the fossil evidence is mostly non-passerine. He considers that for passerines the figures are likely to be very much lower even for the oldest species. This suggests that, at most, the present Asian weavers could only have seen two glaciations and have undergone their radiation entirely within the Pleistocene.

Moreau (in press) has recently completed a re-evaluation of the ecological history of Africa since the Pliocene based upon new geological evidence obtained since his earlier account (1952). During the Pleistocene three glacial periods occurred of which the last continued for at least 50,000 years prior to 18,000 years ago. During this period the temperature of Africa must have been some 5°C. lower than at present at the glacial maximum, and a corresponding reduction in evaporation would have increased the effectiveness of the rainfall. The reduction in temperature would have extended the area of the montane biome down to

between 500 and 1000 metres greatly restricting the lowland biota except in the areas to the west of the Cameroons. The montane avifauna, at present restricted to small isolated areas, would have ranged from the Cameroon Highlands to Abyssinia and to South Africa. Such extension in range must have occurred at each glaciation to be followed by recession and local isolation. In addition sub-regional geological changes, the dating and relationship of which to the glacial changes are not yet understood, occurred. The most significant to the present discussion are the extensions of the Sahael (Sudanese climatic belt) to at least 300 miles north of the present position (on the last occasion only about 7000 years ago) and the southward movement of the palaearctic fauna at least 400 miles into the Sahara.

Changes similar to these must have occurred in both the Arabian and the Indian areas. It seems likely that during each glaciation unbroken palaearctic conditions must have reached southward deeply into Arabia and Persia, in the latter, due to the elevation of the land, penetrating to the coastal strip. In India the whole of the elevated Deccan Plateau was much cooler and more humid and, except where edaphic factors were unsuitable, a Himalayan type of flora and fauna similar to those at present restricted to the Nilgiri Hills, parts of the Western Ghats, the hills of Assam, and the Himalayan foothills (Ali 1949) must have been widespread throughout. Following the glacial maxima the montane biota would have receded giving place to tropical forest in the wetter areas and savannah in the drier or poorer soils (i.e. in Rajasthan and the Deccan traps). At this time a savannah vegetation probably linked Africa through Arabia to India along a rather narrow coastal strip of Persia. The Indo-Gangetic plain was covered by flat land of high water table and presumably flooded for long periods each year. Such seasonal flooding prevents the establishment of a climax swamp forest and great areas of marsh and wet grassland, similar to the uncultivated tarai of today, probably existed.

Archaeological evidence from the Harappa culture (3250-2750 B.C.) and records in stone and literature from Buddhist and ancient Hindu sources (around 2000 years ago) allow a limited reconstruction of the flora (Randhawa 1945, Law 1954). The forests stretched from west to east along the Satpura-Vindhya range (furthest west at Aravalli Hills) and south to the Ajanta area (Hora 1949, Ali 1949, Ripley 1949, 1959a, Dilger 1952) while some probably persisted for a long time in the Indus basin. The forests of the Western Ghats, north central India, and Burma thus formed an unbroken area bordering swamps and grassland in the wet Ganges Valley and savannah in both Rajasthan and to the south in the area of the Deccan traps. Within these forests there must have been sub-divisions into the flora of the cooler more elevated regions, then diminishing in extent, and those of the lower altitudes. Other contrasts



due to the differential distribution of the monsoon rainfall over the area must also have occurred.

The above picture represents a stage in the progressive desiccation which has been going on since the last Ice Age (d' Aubreville 1949, Moreau 1952, Ripley 1959a). The forests of central India have now disappeared and only groves remain (Randhawa 1949). Much of the Ganges Valley is very arid in the dry season.

Similar changes must have occurred in SE. Asia with a major expansion southward of cool climate biota over higher ground at the glacial maxima followed by a recovery of vast tropical forests. In southern Burma, Thailand, and south Indochina the climax forest development was probably prevented over wide areas by prolonged seasonal floods resulting in a grass vegetation (Suvatabandhu 1958, Stamp 1959). During the Ice Ages the islands of Borneo, Java, and Sumatra were connected together with Malaya and Indochina to form the vast continental area of Sundaland. Changes in that land area have been extremely complex (Umbgrove 1949, Beaufort 1951, Dammerman 1929) but most of it must have been covered by rain forest (Richards 1952). In the huge river system draining north over the low-lying land between Malaya and Borneo there were probably patches of open grass-scrub and palms and occasional extensive areas of swamp or grassland maintained on a heavily waterlogged soil. Such areas are more likely than swamp forest because when Sundaland was undivided the climate in the rain shadow to the north of the Sumatra-Javan mountains was probably very much drier than at present with a seasonal rainy period. It follows that, as on the Amazon, the upper reaches of the great northward flowing river contained much swamp grassland rather than the forest that is all to be seen today. Following the Ice Ages the low-lying areas between the present islands were gradually submerged.

The dispersion of the weavers was probably affected by these changes in the following way :

(i) The main eastward movements of the birds probably correlated with the recessions of the last two Ice Ages. During glaciation movement must have been prevented by the southward penetration of the palaeartic biota into Arabia and Persia as well as the expansion of the ' montane ' floras of Africa and Asia. The ensuing savannah conditions in the Middle East must have been ideal for dispersal of seed-eating weavers. During the arid interglacial period, however, desert regions must have constituted a barrier as at present.

(ii) Entry to India would have been much hindered by forest barriers. As these broke up under increasing desiccation the eastward movements, particularly into the Deccan, continued.

(iii) Since only the last two glaciations are considered, it follows that the weavers could have reached Asia following either the last or the

penultimate Ice Age. The Red Sea and Persian Gulf do not appear to have constituted effective barriers. The relict distributions and characteristics (such as the nest form) of *P. megarhynchus* and *P. hypoxanthus* set these species apart from the other Asian birds. They probably represent a distinct and phylogenetically primitive group within the genus, which entered India at the earlier glaciation to be followed later by the more advanced birds of *P. philippinus* type when conditions again became suitable for movement.

Both *P. megarhynchus* and *P. hypoxanthus* are marshland birds and the savannah ancestor is no longer extant. The size contrast is unlikely to be completely explained as an example of Bergmann's Law although *P. megarhynchus* undoubtedly lives in the cooler climate, at least in winter. The upright stance in display and the nest form of *P. megarhynchus* suggest that the use of the tree-top nesting sites is recent following the reduction of swampy marshland.

(iv) The ancestors of *P. philippinus*, *P. manyar*, and *P. benghalensis* presumably spread first into savannah country around the Indus Valley and in Rajasthan. Forest belts doubtless still existed in the Indus basin together with large swamps along the river. The opportunity thus existed for a population to colonise the marshland. A similar region in the Ganges Valley was more certainly cut off from savannah by forests in the Delhi area and to the south. Once weavers had reached the area adaptation to the prevailing marshland would have followed rapidly. Thus at an early date opportunities existed for the development of two marshland populations in the eastern and western limbs of the Indo-Gangetic plain. The relatively greater contrast between *P. benghalensis* and *P. philippinus*, together with the restricted range of the former, suggests that *P. benghalensis* was the first to diverge, probably in the Indus basin. The *P. manyar* stock from the Ganges Valley could have spread eastwards later to colonize the highly suitable marshland areas in SE. Asia by moving along the coasts. It also proved more adaptable than *P. benghalensis* and spread widely over India and Ceylon wherever suitable marshy areas existed.

There are of course several possible alternative explanations. *P. manyar* may have arisen in SE. Asia from a stock ancestral both to it and *P. benghalensis*, or it may represent a second invasion of the Ganges swamp-land at a later date from *P. benghalensis*, when the two had diverged sufficiently for reproductive isolation to have developed. Be this as it may, the main point here is that the local conditions in north India and parts of SE. Asia, in which large swampy basins lay surrounded by forests and at periods effectively isolated from savannah on higher, drier, or poorer land, provided the local isolation during which marshland populations could diverge from the parental savannah stock.

The savannah birds persisted in suitable areas as the ancestors of



*P. philippinus*. Furthermore, as drier conditions developed and savannah spread, the birds ranged widely over India especially in the Deccan.

(v) Prior to the dissolution of Sundaland SE. Asia appears to have contained widely dispersed populations of both *P. hypoxanthus* and *P. manyar*. Later the flooding of the low-lying land between Sumatra, Java, and Borneo seems to have entailed the virtual extinction of most of the weaver populations that lived there. The vast unbroken forests of Malaya, Sumatra, and Borneo would not support a relict population but on drier Java, with its Monsoon climate, a small population of *P. manyar* survived (presumably at first only on the northern alluvial plain), and eventually adapted to the absence of extensive swamps by moving in on a tree nesting site. *P. hypoxanthus* also survived locally on Sumatra and Java.

(vi) The spread of the adaptable and vigorous *P. philippinus* through the forests of SE. Asia seems to be a recent event occasioned by the felling of forests and the opening up of areas to agriculture. It is found now irregularly throughout Malaya (which has no other weavers), Sumatra, and Java, but has not yet reached Borneo where the almost unbroken forests would probably effectively prevent colonisation. In Java *P. manyar* and *P. philippinus* probably compete (see above); the result seems to be the present contrast in altitudinal range and breeding season.

In spite of obvious weaknesses and the paucity of information the above argument does account in general for the facts available and explains the origin of the extant Asian weaver species. During isolation the populations diverged sufficiently in habitat preferences and in reproductive behaviour, so that now that the forest barriers have largely disappeared sympatry occurs without extensive hybridisation. The specific ranking of the birds is certainly justified even though the precise extent of their ecological and behavioural interaction remains to be determined. The degree of competition that occurs is an expression of the continuing unstable relations between the species and their environment.

#### c. The origin and nature of the behavioural differences

The differences between the Asian weavers concern primarily the coloration of the males, habitat preferences, nest sites, and the methods of communication between the sexes by display and voice during pair formation. In particular, contrasts in the orientation of the WBDs and their context within the courtship sequences have been shown to correlate with different motivation in the species concerned. All these contrasting features are fundamentally directed to the guiding of the female to the nest. It is thus the nest site and the nature of the environ-

ment around it which comprise the ultimate factors determining the behaviour shown.

In the tarai contrasts in nest site and communication behaviour are maintained in sympatry in an area of complex interdigitation of species habitats, and it appears that they are genetically controlled and hence innate. However, nest site selection is by no means invariably fixed<sup>1</sup> and, in particular, the contrasts in site between *P. manyar* races on Java and elsewhere suggest that here the factors determining site selection may be sufficiently labile to allow the choice of trees in one locality and rushes in another. The convergence of *P. manyar* in nest site, and probably in courtship, to *P. philippinus* on Java may thus depend on the relative absence of swamp there and the choice of tree sites for nests. Here then the whole shift from the characteristic marshland behaviour of the species could have been due to a direct reaction to the environment. Whether at present the site selection of the Javan population is environmentally or genetically controlled will require much further analysis but the point raises wide issues.

'Genetical systems do not directly and rigidly determine the characteristics of organisms but set up reaction ranges within which those characters develop' (Simpson 1953). Within the labile reaction range the particular character depends upon interaction with the environment. It thus seems probable that the initial adaptation to the grass nest site in a recently invaded (or rapidly changing) environment was due to the differential survival of those members of a population whose site preferences were sufficiently labile to allow the choice of a site, abnormal for the species, but of adaptive significance. Such 'facultative adaptations' dependent upon particular environmental circumstances may be distinguished from 'fixed innate adaptations' determined genetically independently of the environment (Underwood 1954). Furthermore, the learning of the species nest site by the young occupants (i.e. nest site imprinting) may result in the perpetuation of the preference in succeeding generations and the establishment of a tradition (Thorpe 1945, Klopfer 1961). The establishment of such a tradition may allow the selection of genetic changes such that eventually the site preference becomes incorporated into the genotype (i.e. the 'Baldwin effect', Thorpe 1945, Mayr

<sup>1</sup> Note the variation of nest sites chosen by *P. philippinus* in different parts of its range: tall palmyra and date palms near Bombay, vegetation over or hanging within wells near Poona and in the Deccan, trees on canal and stream banks in the tarai, and bungalow verandahs in eastern India and Burma. Even within a given area different sites are chosen in different localities (Crook 1960c, Table I) but the species has never been recorded nesting in rushes or reeds. Similarly occasional records (Hume 1890) describe *P. manyar* and *P. benghalensis* nesting in atypical sites such as low bushes over water rather than in reeds and grass but never in palms or tall trees. In addition Ali (in litt.) informs me that *P. megarhynchus* breeds both in tree-tops and in reed-beds in the same area of the tarai. In this case the preferences cannot be controlled by genetic contrasts as the populations must intermingle in feeding flocks and probably visit both types of site when selecting building places.

1947, Waddington 1953, Simpson 1953, Hinde 1959, Underwood 1954), the behaviour thus becoming 'innate'. This, however, is not essential for the perpetuation of the behavioural change once the tradition is established.

The contrasts in nest site between these three weavers correlate with major differences in the conditions of cover affecting the visibility of the Advertisement displays attracting females to the nest. Thus if a male with a nest hidden in grass continued to display upon it not only would the likelihood of a female seeing him be reduced but the male, often unable to spot the approach of females, might be inhibited frequently from display.

In such a context however the likelihood of neighbouring males seeing one another frequently on their nests is less and the tendency to visit neighbouring nests to steal materials is probably reduced. A reduced frequency of observation of his fellow males is likely to lower the aggressiveness of a territory owner so that the threshold for attack behaviour would rise. This would correlate with a reduced tendency to stay constantly beside the nest and a lowered threshold for approach to females. Displays would thus soon become orientated towards approaching females away from the nest rather than upon or very close to the structure. This could be a simple phenotypic effect of reduced visibility and less territorial trespassing. Furthermore, since the male's display is rarely released without the sight (or sound) of other males in display, and since the performance of display is probably rewarding, particularly if it ends in sex chasing and especially in copulation, the birds may learn to give their displays on grass tops etc. rather than upon the nest, so that a tradition may develop through some such process as 'local enhancement'. Certainly the *P. philippinus* data (Crook 1960c) showing that males sometimes leave their nests on the approach of a female and display upright on twigs indicate that the display orientation is sufficiently labile to allow the development of a facultative adaptation here. Further shifts in orientation so that the display comes to be given following an approach flight to the female could develop in the same way.

This approach could account for the present differences in pair formation behaviour between *P. philippinus*, *P. manyar*, and *P. benghalensis*. *P. philippinus*, a highly successful dry country stock responding fully to the climate changes favourable to it in the present epoch, retains the original inverted nest-oriented type of advertisement at the tree nest-site. In *P. manyar*, nesting in rushes and reed-beds scattered over swamps, the relatively loose character of the vegetation appears to have permitted the retention of display near the nest so that it still functions as a territorial proclamation. The dense grass in which *P. benghalensis* places its nest makes approach to the female a necessity if initial contact between the sexes is to be established. The display here becomes purely of courtship



function and in correlation with this the song is much subdued. Furthermore the motivational contrasts between the three species in the tarai (pp. 26-29) are also explained.

In Java the local race of *P. manyar* places its nests in trees with good visibility all around. As a result the behaviour of the bird probably resembles that of *P. philippinus* extremely closely.

The important question then is to determine the limits of lability of nest site selection in each species for it is this that very largely determines the types of pair formation behaviour (Crook 1962). Thus, while *P. philippinus* chooses a wide range of sites in different localities, the conditions of visibility around the nests remain about the same and the communication system between the sexes in reproductive behaviour is not affected as it would be if a local population suddenly took to the reeds. In the case of the Java population of *P. manyar* the change does involve a major increase in visibility which probably has affected the signal system. Here then the lability of site selection appears to have been larger than for *P. philippinus* and has probably had more severe consequences. In the Kumaon tarai, in spite of the mixture of habitats, each species shows clear nest-site preferences suggesting that the range is fairly tightly controlled. There is, however, probably sufficient lability to allow quite a drastic change of site should the birds be confined to a habitat radically different to the preferred one. The effect of such a change, which might be arranged experimentally, on the orientation of the WBD would be extremely interesting to observe.

Finally, while the stereotyped appearance of the ritualised displays (Tinbergen 1952, Blest 1961, Crook 1962) in advertisement must be the result of sexual selection, differences in the posture material, upon which selection has worked in producing the signal, may well have been determined initially by shifts in the strengths of tendencies to remain at the nest and to approach the female of the type described above.

Thus while characters such as plumage coloration, body size, beak proportions, nest structure, and ritualised wing beating displays have narrow reaction ranges, other characteristics such as nest-site selection, the orientation of the displays, and the sequence of events in courtship are probably more labile and, through their adaptability, allow rapid phenotypic adaptation to invaded or changing environments. It follows that some 'fixed adaptations', such as the ritualised displays, may be dependent for their orientation and function on facultative adaptations perhaps maintained by local or specific traditions.

#### d. Species grouping

Moreau (1960) placed the Asian Ploceines in two separate species groups of the genus *Ploceus*, the first consisting of *P. manyar*, *P. philippinus*, *P. benghalensis*, and *P. megarhynchus* and the second of *P. hypoxan-*



thus together with the African species *Ploceus (Pachyphantes) superciliosus*. This latter group was established mainly upon supposed similarities in nest structure, which a close reading of the literature taken in conjunction with new observations in Africa on the nest form and construction of *P. superciliosus* (Crook in preparation) now show to be invalid. Since Moreau's account the new data on *P. megarhynchus* has also become available. In the above survey it is shown that while *P. philippinus*, *P. manyar*, and *P. benghalensis* are extremely similar to one another, *P. megarhynchus* and *P. hypoxanthus* resemble one another much more than either resembles the *manyar* group. It is thus considered that the two species groups of the genus *Ploceus* found in Asia be composed as follows: (1) *Ploceus megarhynchus* and *P. hypoxanthus*, (2) *Ploceus manyar*, *P. philippinus*, and *P. benghalensis*. Neither appears to have any close relationship with any well-studied African species group.

## V. SUMMARY

(i) In many areas of tropical Asia several closely related Ploceine species show sympatric distributions. The problems of reproductive isolation and competition posed by these species are discussed. New field data on *Ploceus benghalensis* and *Ploceus manyar* observed in the Kumaon tarai 1959 are provided, and the characteristics of these and other Asian weavers are summarised in Tables II and III.

(ii) The available data suggest:

(a) *Ploceus megarhynchus* and *P. hypoxanthus*, which differ greatly in body size, bill proportions, coloration, nest form and site, and behaviour (still unknown for *hypoxanthus*) from other Asian weavers, are only distantly related to them and would under no circumstances in the wild interbreed or compete with them.

(b) *P. philippinus*, *P. manyar*, and *P. benghalensis*, probably take similar or identical foods and compete for nourishment in areas of sympatry under conditions of food shortage. Differences between the species in habitat preferences in the breeding season and 'superabundance' of food in at least part of the dry season probably limits the frequency and duration of periods of competition. Actual measures are required.

(c) The six contrasting variables likely to play a role in ensuring reproductive isolation between *P. philippinus*, *P. manyar*, and *P. benghalensis* are: (i) coloration of nuptial males, (ii) sequence of events in courtship, (iii) postures, orientation and vocalisation during Wing Beating Display, (iv) nest site, (v) nest form and fabric, and (vi) habitat. The first four are the more important—in particular the orientation of WB display postures, which is closely correlated with differences in nest sites. The females perform mate selection so that attempts by males in mixed colonies to mount females other than those of their own species are not, by themselves, of much biological significance. Deliberate female

choice of male, nest, and site of a species other than her own has yet to be recorded.

(iii) The ancestors of the Asian weavers entered Asia from Africa as savannah-adapted birds. Radiation into swamp and grassland species has occurred in isolation within Asia. Evidence from nest structures and sites, comparative behaviour, and, in particular, the few available studies of vegetation changes in Asia since the Pliocene, is used to produce a hypothesis for the radiation and speciation of the birds. The relative importance of 'innate' and 'traditional' behaviour in the maintenance of specific characters is briefly discussed.

The Asian weavers are listed in two groups : (a) *Ploceus megarhynchus* and *P. hypoxanthus* ; (b) *P. philippinus*, *P. manyar*, and *P. benghalensis*. Neither appears to have any particularly close relationship with any existing African species group of the genus.

#### ACKNOWLEDGEMENTS

Without the encouragement and assistance of many persons these studies could never have been made. First and foremost I owe much to Dr. Sálím Ali, who not only took a great personal interest in these studies but also arranged and participated in the expedition to Kumaon. Dr. Ali's great knowledge of the Asian Ploceinae has been a major source of information and he has helped to mould many of the ideas presented here. It was largely due to him that my visit to India became possible and without his help and advice it would have been most difficult to obtain satisfactory results.

During the Kumaon trip the co-operation of the Chief Conservator of Forests, U.P., and officers of his department, in particular Shri S. S. Bahadur, Wild Life Warden, Western Circle, was deeply appreciated. Further in India, I have benefited from working in the field with Shri Vijaykumar Ambedkar who did much to help me with investigations on the Baya in the Poona area, and with whom I have had many interesting discussions. I am also grateful to Drs. Telford Work, C. Anderson, Harold Trapido, and Raja Varma, all of the Virus Research Centre, Poona, who took an interest in the work and in various ways assisted me during my stay with them. I greatly appreciated the use of V.R.C. facilities. Mr. John Goatly, regional representative of the British Council in Bombay, helped me greatly over certain problems.

In Cambridge Dr. W. H. Thorpe, F.R.S., and Dr. Robert Hinde have discussed the work with me at various stages and helped me greatly with their advice and encouragement. Dr. N. Tinbergen, F.R.S., kindly read through the manuscript in preparation and commented upon it. In addition Dr. E. J. H. Corner and Mr. Peter Ashton of the Cambridge Botany School helped me over certain questions. I am indebted to Mr. A. M. Walker for statistical advice. The studies were financed by the

Department of Scientific and Industrial Research, London, without whose assistance the work could never have been done.

## REFERENCES

- Abduali, H. (1960) : A new race of Finn's Baya, *Ploceus megarhynchus* Hume. *J. Bombay nat. Hist. Soc.* **57** : 659-662.
- Ali, Sálím. (1931) : The nesting habits of the Baya (*Ploceus philippinus*). *J. Bombay nat. Hist. Soc.* **34** : 947-964.
- (1949) : The Satpura trend as an ornitho-geographical highway. *Proc. Nat. Inst. Sci. India* **15** (8) : 379-386.
- , & Ambedkar, V. C. (1956) : Notes on the Baya weaver bird, *Ploceus philippinus*. *J. Bombay nat. Hist. Soc.* **53** : 381-389.
- (1957) : Further notes on the Baya weaver bird, *Ploceus philippinus*. *J. Bombay nat. Hist. Soc.* **54** : 491-502.
- , & Crook, J. H. (1959) : Observations on Finn's Baya (*Ploceus megarhynchus* Hume) rediscovered in the Kumaon Tarai 1959. *J. Bombay nat. Hist. Soc.* **56** : 457-483.
- Ambedkar, V. C. (1958) : Notes on the Baya : Breeding season 1957. *J. Bombay nat. Hist. Soc.* **55** : 100-106.
- Andrew, R. (1961) : The displays given by passerines in courtship and reproductive fighting : a review. *Ibis* **103a** : 315-348 ; 549-579.
- Aubreville, A. d' (1949) : Climat, forêts et desertification de l'Afrique tropicale. Paris.
- Baker, E. C. Stuart (1926) : The Fauna of British India, Birds 3. London.
- (1934) : The nidification of Birds of the Indian Empire. London.
- Beaufort, L.F. de (1951) : Zoogeography of the land and inland waters. London.
- Blest, D. (1961) : The Concept of ritualisation, in 'Current problems in Animal Behaviour', ed. W. H. Thorpe and O. L. Zangwill. Cambridge.
- Brodkorb, P. (1960) : How many species have evolved? *Bull. Florida State Mus.* **5**(3) : 41-53.
- Chapin, J. P. (1923) : Ecological aspects of bird distribution in tropical Africa. *Amer. Nat.* **57** : 106-124.
- Crombie, A. C. (1947) : Interspecific competition. *J. Anim. Ecol.* **16** : 44-73.
- Crook, J. H. (1959) : Behaviour study and the classification of West African weaver birds. *Proc. Linn. Soc. Lond.* 170 session : 147-153.
- (1960a) : Nest form and construction in West African weaver birds. *Ibis* **102** : 1-25.
- Crook, J. H. (1960b) : Studies on the social behaviour of *Quelea q. quelea*, in French West Africa. *Behaviour* **16** : 1-55.
- (1960c) : Studies on the reproductive behaviour of the Baya Weaver (*Ploceus philippinus*). *J. Bombay nat. Hist. Soc.* **57** : 1-44.
- (1962) : The adaptive significance of pair formation types in weaver birds. 8th Symposium Zool. Soc. London.
- (in press) : Comparative studies on the reproductive behaviour of two closely related weaver birds (*Ploceus cucullatus* and *P. nigerrimus*) and their races. *Behaviour*.
- Dammerman, K. W. (1929) : On the Zoogeography of Java. *Treubia* **2** : 1-88.
- Darlington, P. J. (1957) : Zoogeography : the geographical distribution of animals. New York.
- Delacour, J. (1947) : Birds of Malaysia, New York.
- Dilger, W. C. (1952) : The Brij hypothesis as an explanation for the tropical faunal similarities between the Western Ghats and the Eastern Himalayas, Assam, Burma, and Malaya. *Evolution* **6** : 125-127.
- Dobzhansky, T. (1941) : Genetics and the origin of species (2nd Ed.). New York.
- Gause, G. F. (1934) : The struggle for existence. Baltimore.
- Gray, A. P. (1958) : Bird Hybrids. C.A.B. England.
- Hall, M. F. (1962) : Evolutionary aspects of estrildid song. 8th Symp. zool. Soc. Lond. : 37-55.
- Hinde, R. (1953) : The conflict between drives in the courtship and copulation of the Chaffinch. *Behaviour* **5** : 1-31.
- (1955-56) : A comparative study of the courtship of certain finches. (Fringillidae). *Ibis* **97** : 706-754 ; **98** : 1-23.
- (1959) : Behaviour and speciation in birds and lower vertebrates. *Bio. Revs.* **34** : 85-128.
- Hoogerwerf, A. (1947) : Contribution to the knowledge of the distribution of birds on the island of Java. *Treubia* **19** : 83-137.
- Hora, S. L. (1949) : Satpura hypothesis of the distribution of the Malayan fauna and flora to peninsular India. *Proc. Nat. Inst. Sci. India* **15**(8) : 309-314.



- Hume, A. O. (1890): The nests and eggs of Indian birds (Ed.: E. W. Oates) Vol. II. London.
- Husain, K. Z. (1958): Subdivisions and zoogeography of the genus *Treron* (Green fruit pigeons). *Ibis* 100: 334-348.
- Huxley, J. S. (1942): Evolution, the modern synthesis. London.
- Jerdon, T. C. (1877): The birds of India ... Vol. 2. Calcutta.
- Kear, J. (1962). Food Selection in finches with special reference to inter-specific differences. *Proc. Zool. Soc. Lond.* 138: 163-203.
- Klopfer, P. H. (1961): Observational learning in birds: the establishment of behavioural modes. *Behaviour* 17: 17-79.
- Lack, D. (1944): Ecological aspects of species formation in passerine birds. *Ibis* 86: 260-286.
- (1954): The natural regulation of animal numbers. Oxford.
- Law, B. C. (1954): Historical geography of Ancient India. Paris.
- Mackenzie, J. M. D. (1916): The nidification of the Golden Weaver bird. *J. Bombay nat. Hist. Soc.* 24: 821.
- Marshall, A. J. (1959): Internal and environmental control of breeding. *Ibis* 101: 456-477.
- Mayr, E. (1942): Systematics and the origin of species. New York.
- (1947): Ecological factors in speciation. *Evolution* 1: 263-288.
- Moreau, R. E. (1948): Ecological isolation in a rich tropical avifauna. *J. anim. Ecol.* 17: 113-126.
- (1952): Africa since the Mesozoic, with particular reference to certain biological problems. *Proc. Zool. Soc. Lond.* 121: 869-913.
- (1960): Conspectus and classification of the Ploceine weaver birds. *Ibis* 102: 298-321; 443-471.
- (In press): Vicissitudes of the African biota in the late Pleistocene. *Proc. Zool. Soc. Lond.*
- Morel, G., Morel, Y., & Bourliere, F. (1957): The blackfaced weaver bird or Dioch in West Africa. An ecological study. *J. Bombay nat. Hist. Soc.* 54: 811-825.
- Morris, D. (1952): The reproductive behaviour of the Zebra finch (*Poephila guttata*) with special reference to pseudo-female behaviour and displacement activities. *Behaviour* 6: 271-322.
- (1956): The feather postures of birds and the problem of the origin of social signals. *Behaviour* 9: 75-113.
- Oates, E. W. (1883): A handbook to the birds of British Burma .... Vol. I. London.
- Randhawa, M. S. (1945): Progressive desiccation of northern India in historical times. *J. Bombay nat. Hist. Soc.* 45: 558-565.
- Richards, P. W. (1952): Tropical Rain Forest. Cambridge.
- Ripley, S. Dillon (1949): Avian relicts and double invasions in peninsular India and Ceylon. *Evolution* 3: 150-159.
- (1954): Comments on the bio-geography of Arabia with particular reference to birds. *J. Bombay nat. Hist. Soc.* 52: 241-248.
- (1959a): Zoogeographic considerations on the Indian Avifauna. *J. Bombay nat. Hist. Soc.* 56: 72-81.
- (1959b): Competition between sunbird and honeyeater species in the Moluccan Islands. *Amer. Nat.* 93: 127-134.
- Selander, R. K., & Giller, D. R. (1961): Analysis of sympatry of Great Tailed and Boat Tailed Grackles. *Condor* 63: 29-86.
- Simpson, G. C. (1953): The Baldwin effect. *Evolution* 7: 110-117.
- Skead, C. J. (1947): A study of the Cape Weaver (*Hyphantornis capensis olivaceus*). *Ostrich* 18: 1-42.
- Smythies, B. E. (1953): The Birds of Burma (2nd ed.). London.
- Spennemann, A. (1926): Iets over *Ploceus manyar*. *De Tropische Natuur*. 1926: 186-189.
- Stamp, L. D. (1959): Asia: a regional and economic geography. London.
- Suvatabandhu, K. (1958): Vegetation of Thailand and its correlation with climate and soil type. *Proc. Symposium on Humid Tropics vegetation. Indonesia, 1958, UNESCO.*
- Thorpe, W. H. (1945): The evolutionary significance of habitat selection. *J. anim. Ecol.* 14: 67-79.
- (1952): 'Derived activities'; their causation, biological significance, origin and emancipation during evolution. *Quart. Rev. Biol.* 27: 1-32.
- Tinbergen, N. (1959): Comparative studies of the behaviour of Gulls (Laridae): a progress report. *Behaviour* 15: 1-70.
- Umbgrove, J. H. F. (1949): The structural history of the East Indies. Cambridge.
- Underwood, G. (1954): Categories of adaptation. *Evolution* 8: 365-377.
- Waddington, C. H. (1953): The 'Baldwin effect', 'genetic assimilation' and 'homeostasis'. *Evolution* 7: 386-387.
- Whistler, H. (n.d.): MS., quoted by Sálím Ali, (in litt.)
- Wynne-Edwards, V. C. (1959): Control of population density through social behaviour. *Ibis* 101: 436-441.